Comparative Study of the Floral Morphology and Anatomy in Anacardiaceae, Burseraceae, and Kirkiaceae (Sapindales)

Dissertation
zur
Erlangung der naturwissenschaftlichen Doktorwürde
(Dr. sc. nat.)
vorgelegt der
Mathematisch-naturwissenschaflichen Fakultät
der
Universität Zürich
von
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aus
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Promotionskomittee

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Zürich, 2009

Int. J. Plant Sci. 168(9):1237–1253. 2007.

1058-5893/2007/16809-0002$15.00 DOI: 10.1086/521795

DEVELOPMENT OF INFLORESCENCES, CUPULES, AND FLOWERS IN *AMPHIPTERYGIUM* AND COMPARISON WITH *PISTACIA* (ANACARDIACEAE)

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Amphipterygium was originally placed in its own family, Julianiaceae, mainly because of its unique infructescences, which form samaroid dispersal units containing a single fertile, one-seeded fruit and three or more sterile fruits enclosed in a cupulelike structure. Its position in Anacardiaceae-Anacardioideae and a close relationship with *Pistacia* were suggested by structural and chemical features, and the position of both genera in Anacardioideae was recently supported by molecular phylogenetic studies. However, the development and structure of these infructescences and flowers have never been analyzed and comparatively studied. This study shows that each samaroid structure in *Amphipterygium* is a few-flowered cyme and that the teeth at the entrance of the cupule are the subtending bracts of the flowers. A comparison of *Amphipterygium* with *Pistacia* also shows that both genera share with *Rhus* and other genera of Anacardioideae a tricarpellate, pseudomonomerous gynoecium with a unilocular ovary and a single crassinucellar and (hemi)anatropous ovule with a ponticulus. However, the ovules in both *Amphipterygium* and *Pistacia* are outstanding in being unitegmic (though sometimes with traces of a second integument on the convex side) and having a massive funicle with unique lateral and median outgrowths, which becomes much larger than the ovule after anthesis. The funicle is also proportionally much larger and more complicated in shape than that of all other Anacardiaceae studied. In addition, both genera are wind pollinated and thus exhibit similar evolutionary trends, such as dioecy, reduction of perianth (lack of petals and, at least in part, also of sepals), large (bilobed) stigmas with multicellular papillae, and similar pollen. It is not yet clear whether wind pollination evolved separately in each genus or only once in their common ancestor. However, the inclusion of *Amphipterygium* within Anacardioideae is strongly supported by floral reproductive structures.

Keywords: *Amphipterygium*, Anacardiaceae, Anacardioideae, cupule, floral morphology, funicle, gynoecium, ovule, *Pistacia*, pseudomonomery, Rhoeae, samaroid.

Introduction

Amphipterygium was originally a member of Julianiaceae, a small Neotropical family of dioecious, wind-pollinated, and deciduous shrubs to small-sized trees, which was erected by Hemsley (1906, 1907) because of its unique infructescences. Julianiaceae comprised *Orthopterygium* Hemsley et Rose, a monospecific genus endemic to Peru, and *Amphipterygium* Standl., represented mainly by the Central American *Amphipterygium adstringens* (Schltdl.) Standl. and a few other doubtful species known only from scarce collections, mainly from Mexico (Gray 1854; Hemsley 1901, 1906, 1907; Hemsley and Rose 1903; Standley 1923; Pennington and Sarukhán 1968; Holdridge and Poveda 1975; Medina 2000).

Amphipterygium was first described as *Hypopterygium adstringens* (Schlechtendal 1843*b*) and subsequently as *Juliania* (Schlechtendal 1843*a*). Schlechtendal (1843*b*, p. 635) noted that the shapes of the style and stigmas of the female flowers were reminiscent of those of Anacardiaceae, especially *Pistacia*, but also regarded the genus as the "potential type of a new order with multiple affinities." Its unusual female inflorescence, "consisting of an almost closed, usually five-toothed involucre, borne on a flattened pedicel and containing three [*Orthopterygium*] to four [*Amphipterygium*] collateral flowers, of which the two outside ones are, perhaps, always abortive," led Hemsley (1906, pp. 231, 232–234) to compare Julianiaceae with Fagaceae and Juglandaceae, in addition to Anacardiaceae. He found most similarities with Juglandaceae and Fagaceae. Kershaw (1909) also supported a closer affinity of Julianiaceae and Juglandaceae by stating that the single unitegmic ovule per flower of *Amphipterygium* and *Juglans* (described by Nicoloff 1904 and Boodle in Hemsley 1907) shared a homologous obturator and suggested that the anatropous ovule in *Amphipterygium*, with one obturator (for term, see Endress 1994), was derived from the orthotropous ovule with two obturators of Juglandaceae, one having been lost with the bending of the ovule.

However, Hemsley (1907, p. 192) emphasized that on the basis of anatomical characters, Julianiaceae "would have to be placed next to the Anacardiaceae." Fritsch (1908) noticed that the resin canals developed identically in the phloem throughout the plant in Julianiaceae and Anacardiaceae and that the structure of the ovary and the ovule agreed in both families. Hallier (1908) even supposed a direct evolutionary origin of *Amphipterygium* from *Pistacia* (without providing a detailed comparison). Later, Copeland and Doyel (1940) emphasized

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Manuscript received March 2007; revised manuscript received July 2007.

that the ovule orientation and its vascular supply, plus the presence of a hypostase, supported close relationships of Julianiaceae with Anacardiaceae and not with Juglandaceae. Comparative wood anatomy showed similar secondary xylem in the two families (Copeland and Doyel 1940; Stern 1952). Further, because of the number of stigmas, Stern (1952) emphasized that the flowers of Julianiaceae were tricarpellate, as were those of many members of Rhoeae in Anacardiaceae, whereas those of Juglandaceae were bicarpellate.

Flavonoid chemistry indicated that Julianiaceae represent a subtribe of Rhoeae of Anacardiaceae (Young 1976). This was further supported by serotaxonomy (Petersen and Fairbrothers 1983) and endocarp structure (Wannan and Quinn 1990). Phylogenetic studies consistently support placement of Julianiaceae within Anacardioideae (Anacardiaceae), in a subclade with *Pistacia* (fig. 1) (*rps*16, *trn*L-F, Pell 2004; *rbc*L and nonmolecular characters, Aguilar-Ortigoza and Sosa 2004; Wannan 2006).

However, the structural basis of the puzzling winged (samaroid) and cupulate one-seeded infructescences of *Amphipterygium* is still unknown, and its floral structure and development have never been studied in detail. Also, a detailed comparison of *Amphipterygium* with any other representative of Anacardiaceae has never been carried out. It is the goal of this study to tackle these unanswered questions.

Material and Methods

The following material was studied: *Amphipterygium adstringens* (Schltdl.) Schiede, female: D.H. Lorence, 5025 (Sierra Tepozteco, Morelos, Mexico); R. Manzanell, s.n. (09 Aug. 1975; Guatemala); R. Torrès C., 8776 (s.d.; Mexico); male: P.K. Endress 96-21 (07 Aug. 1996; National Tropical Botanical Garden, Kauai, Hawaii, USA); *Pistacia atlantica* Desf., female: P.K. Endress, s.n. (04 May 1971, Algeria); *Pistacia lentiscus* L., female: J.B. Bachelier, 04-04 (several collections of the same specimen, before, during, and after flowering time, 2004 and 2005; La Motte-en-Provence, Var, France); P.K. Endress, 5318 (09 May 1981; cult. Isole di Brissago, Switzerland); male: J.B. Bachelier, 05-04 (06 Jun. 2004; cult., Botanic Garden of the University of Zurich); *Pistacia mexicana* H.B.K., female: P.K. Endress, 1401 (05 March 1969; Chiapas, Mexico); *Pistacia terebinthus* L., female: P.K. Endress, s.n. (26 March 1971; Rhodos, Greece); *Pistacia vera* L., female: P.K. Endress, 4475 (20 May 1978; cult., E. Frey, Ronco, Switzerland).

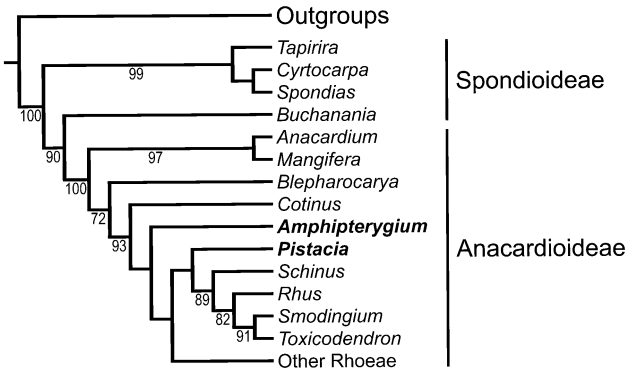

Fig. 1 Phylogeny of Anacardiaceae, based on a combined analysis using *rbc*L and nonmolecular data (simplified after Aguilar-Ortigoza and Sosa 2004). Jackknife values above 70% are indicated.

All flowers and infructescences, fixed in FAA or 70% ethanol, were studied using light microscopy (LM) and scanning electron microscopy (SEM). For LM investigations, the plant material was infiltrated and embedded in Kulzer's Technovit 7100 (2-hydroxyethyl methacrylate), following a protocol adapted from those of Igersheim (1993) and Igersheim and Cichocki (1996). The embedded material was sectioned at 5, 7, or 10 μm, depending on the parts, using a Microm HM 355 rotary microtome and a standard microtome knife D. Following the adapted protocol of Weber and Igersheim (1994), the sections were stained with ruthenium red and toluidine blue (both from Fluka) and mounted in Histomount.

For SEM investigations, specimens were treated with 2% osmium tetroxide (Fluka), dehydrated in ethanol and acetone, critical-point dried and sputter-coated with gold, and studied at 20 kV with a Hitachi S-4000 scanning electron microscope. All vouchers and permanent slides of serial microtome sections are deposited at Z.

Results

Female Inflorescence and Infructescence of Amphipterygium

Female inflorescences begin to develop in the axil of very young leaves (fig. 2*A*) but remain hidden for some time, tightly appressed to and basally fused with the petiole (fig. 2*A*). The anthetic inflorescence is inconspicuous because of its color and indument, which are similar to those of the now longer leaves and petioles (see Hemsley 1906, 1907; Fritsch 1908). The maturing infructescences are commonly clustered together at the end of leafless shoots (fig. 2*A*, 2*B*).

Each female inflorescence comprises one or two units formed laterally on a short shoot, which ends in an undifferentiated bud. Each unit develops into a samaroid structure with a flattened peduncle and a distal involucre, which mostly contains four flowers. When two samaroid units are present, they develop parallel to each other. A subtending bract (B1) is present at the base of the abaxial face of the flattened peduncle of each samaroid unit, and the terminal bud of the inflorescence shoot is present between their adaxial faces (fig. 2*B*, 2*C*). The two samaroid units alternate, and the lower one is often larger and further advanced in development than the upper (fig. 2*B*, 2*C*). Hairs are present except in the locule, on the ovule, and on the stigma. They may be simple (unicellular or uniseriate 2–5 cellular) or glandular, with a short stalk and a multicellular head (see also Fritsch 1908).

The peduncle of each samaroid unit enlarges and becomes conspicuously flattened above B1. At anthesis, each peduncle ends in a globose involucre with a narrow circular aperture on top, surrounded by five teeth (fig. 2*C*). Each involucre contains four (rarely five) collateral flowers of different sizes, the centralmost flower (F1) being the largest and the other three (or four) gradually smaller (fig. 2*D*–2*F*).

The second-largest flower (F2) is located between F1 and F4 (fig. 2). F1 is the oldest flower and commonly also the only

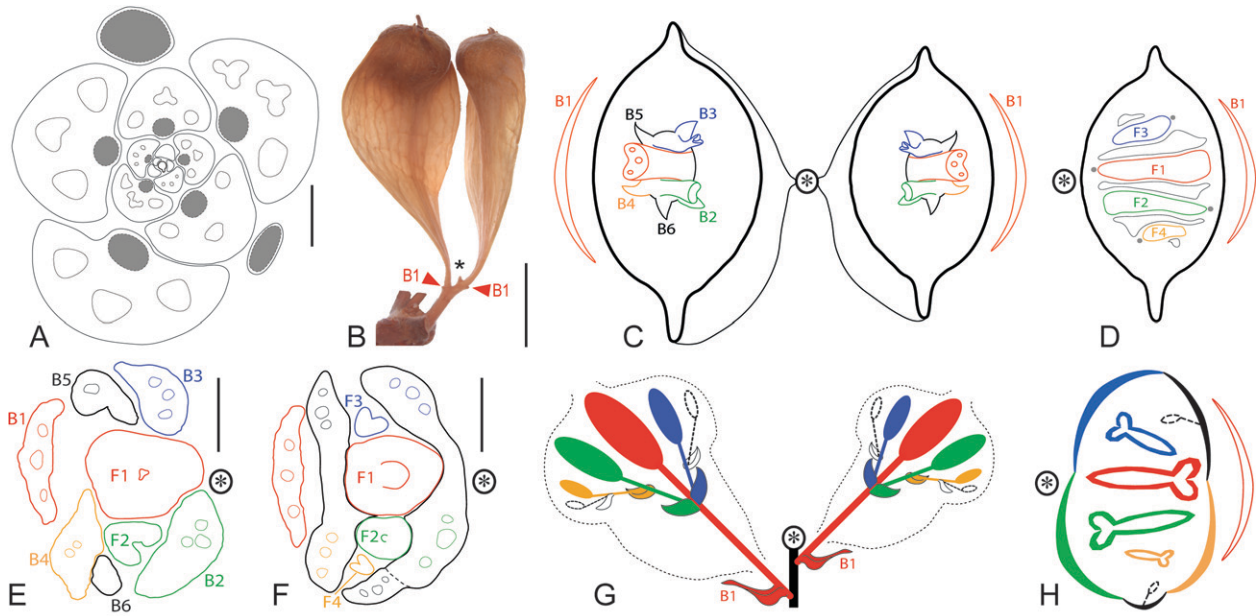

Fig. 2 *Amphipterygium adstringens*. Female inflorescences and infructescences. Each flower and its subtending bract are marked with a specific color. For instance, red corresponds to flower F1 and its subtending bract B1. Scale bars: $A = 1$ mm; $B = 1$ cm; $E, F = 0.2$ mm. *A*, Transverse section (TS) of a flowering shoot, with spiral arrangement of leaves and inflorescences. Gray parts represent the vasculature in the base of two postanthetic inflorescence axes and the vasculature trace of seven preanthetic inflorescences in the base of their subtending leaves, with which they are fused. *B*, Mature infructescence comprising a pair of alternate samaroid units. The lower samaroid unit is larger than the upper one. Red arrowheads point to the scar of B1, and the asterisk indicates the position of the undifferentiated bud terminating the inflorescence main axis. *C*, Same infructescence, from above, showing position of bracts (*B1–B6*) and remains of styles on each samaroid unit. Note their regular arrangement in and around the narrow circular opening of the involucre (cupule). The structure of the larger samaroid unit (on the left) follows the left pattern (L) and mirrors that of the smaller samaroid unit (on the right), which follows the right pattern (R). *D*, Schematic TS of a samaroid unit (R). Collateral fruits (*F1–F4*) are spaced by lacunae within the involucre (cupule). Fruit position and ovule orientations alternate in the involucre (cupule). Dorsal vascular bundle of each fruit is marked with gray dot (cf. TS series in fig. 4). *E*, *F*, TS series of a very young (preanthetic) samaroid unit (L), showing orientation of flowers with regard to the bracts and how the bases of B2–B6 fuse together to form the rim of the involucre (cupule) around the collateral flowers. *G*, Inflorescence branching pattern. Each samaroid unit is a few-flowered cyme, and the whole inflorescence is a thyrse. The thick dashed lines represent the commonly not developing flowers associated with B5 and B6; the thin dashed lines indicate the outline of the samaroid units. *H*, Schematic diagram of a samaroid unit (R) (corresponding to *D*), showing the collateral arrangement of flowers in the involucre (cupule) and their position with regard to their floral subtending bract. The thick dashed lines represent the commonly not developing flowers associated with B5 and B6.

flower out of the four (five) that fully develops its style and three stigmas through the aperture of the involucre (fig. 3). After anthesis of F1, the samaroid unit enlarges considerably along its transverse plane of symmetry, and the globose shape of the involucre becomes more ovoid and its base thicker. On top of the involucre of the ripening samaroid unit, remains of usually three (sometimes two or four) abscised styles or reduced stigmas indicate that the other flowers continue to develop after anthesis of F1 and that their delayed and often imperfect stigmas can also reach the aperture (figs. 2*C*, 4*G′*). Nevertheless, normally only F1 produces a mature fruit with a single seed. The other fruits are normally sterile and contain a modified ovule without an embryo (Hemsley 1906, 1907; Fritsch 1908).

One or two transverse (alternate) bracts are initiated at the inflorescence apex and initially protect it. These two bracts are the subtending bracts (B1) of future samaroid units. Their development begins in the axil of B1 by the initiation of two additional bracts (B2 and, later, B3), which develop on the adaxial side of the samaroid unit and face B1. The first flower (F1), apparently in the axil of B1, is formed between B2 and B3, which are thus interpreted to be the prophylls of F1. A fourth and a fifth bract (B4 and B5) are initiated more or less above B1 and face B2 and B3, respectively. Two collateral flowers (F2 and, later, F3), apparently in the axils of B2 and B3, respectively, begin to develop on each side of F1 (fig. 5*A*). The bases of B2–B5 are united together and begin to form the involucre of the capitulum of flowers, with the free ends of B2 and B3 bent over B4 and B5, respectively.

Between the bract pairs B2/B4 and B3/B5, F1 is compressed by the growth of F2 and F3 on its sides. The structure of the samaroid unit is now monosymmetric (for term, see Endress 1999), with a median plane of symmetry matching that of F1. The successive development of the last bract, B6, between B2 and B4, and of the last flower, F4, initiated between B4 and B6 and interpreted to be in the axil of B4, completes its structure, which is now asymmetric (fig. 2*E*, 2*F*).

During development of the capitulum, the growth of the involucre draws the floral bases upward along the former median plane of symmetry of the samaroid unit. Thus, each flower, especially F1 and F2, participates in the formation of the inner wall of the involucre and becomes more or less flattened

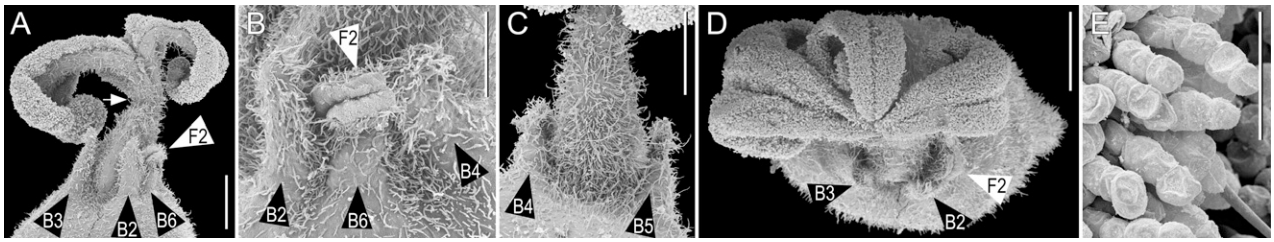

Fig. 3 *Amphipterygium adstringens*. Anthetic samaroid unit and female flowers. Black arrowheads point to bracts (*B2–B6*); white arrowheads point to flower (*F2*). Scale bars: *A*, *D* = 1 mm; *B* = 0.5 mm; *C* = 0.8 mm; *E* = 80 μm. *A*, Samaroid unit (right pattern), from lateral. Style and stigmas of the first flower (*F1*) are fully developed and exserted through the aperture on top of the involucre (cupule). One of the stigmas of the second flower (*F2*) starts to be exposed as well. The white arrow points to constriction on the style of F1 where abscission of the upper part will take place after anthesis. *B*, Same samaroid unit, close-up of F2. *C*, Same samaroid unit, lateral view, side opposite to that in *A*. *D*, Same samaroid unit, from above. The three stigmas of F1 form a short (external) compitum where they unite with each other. Note that the stigmatic lobes of F1 are twisted out of their original positions; the stigmatic lobe of the fertile carpel is on the left side. *E*, Same samaroid unit, close-up of the multicellular stigmatic papillae.

at right angles to the flattened peduncle (fig. 4*H′*, 4*I′*). In contrast, the now broader faces of the collateral flowers remain free during development of the involucre, resulting in the formation of slit-shaped "cavities" between the flowers (figs. 2*D*, 4*H′*–4*O′*). The united bases of the five bracts (B2–B6), which first formed the rim of the involucre, later form the ringlike aperture on top of it. Thus, the five teeth described by Schlechtendal (1843*b*) correspond to the free ends of these five bracts (figs. 2*H*, 4*G′*–4*O′*).

In each capitulum, the arrangement of the collateral flowers and the floral subtending bracts appears very regular with regard to the position of F1. The side of the samaroid unit on which the even-numbered flowers (F2 and F4) and floral subtending bracts (B2, B4, and B6) develop is commonly more convex in mature infructescences than the side with the odd numbers (fig. 2*C*). In addition, ovule orientation exhibits a regular pattern, in F1 and F4 toward the adaxial side of the samaroid unit and in F2 and F3 toward the abaxial side (fig. 2*H*). Flower orientation within each capitulum is also related to the position of the samaroid unit on the inflorescence shoot. Thus, there are two morphs of samaroid units that mirror each other in their symmetry, called here "L" (left) and "R" (right) (fig. 2*C*).

The alternating flower orientation within each capitulum, combined with the delayed sequence of development and the production of a single seed (by F1), indicates that F1 is the terminal flower of the main axis of each samaroid unit. The collateral flowers F2 and F3 terminate the axes of the second branching order of each samaroid unit, and F4 is a flower of the third branching order. Pedicels are lacking, and the floral bases contribute to the expanding base of the involucre. In rare cases, a seventh bract (B7) and a fifth flower (F5) are formed in positions that correspond to the symmetric projections of B6 and F4 with regard to F1. Thus, the structure of each samaroid unit appears to be a few-flowered cyme with a dichasial (F2 and F3) and a monochasial (F4, rarely F5) part, and, consequently, the whole inflorescence, composed of two samaroid units, is a thyrse (fig. 2*G*).

If two samaroid units develop, they are always an L and an R morph. This is expressed by the flower position and ovule orientation with regard to the position of B1, the convex narrow side of the samaroid unit, or the position of the five teeth around the aperture on top of the involucre (fig. 2*C*).

Female Flower of Amphipterygium

The description of the morphology and development of the female flower and ovule is based on F1 because it is the single fertile flower (fig. 4). Aberrant features for the other flowers will be indicated if of interest.

The flowers lack a perianth and an androecium and consist of a sessile gynoecium with a flattened ovary and a massive style ending in three bilobed stigmas. The ovary is unilocular, as only one of the three carpels is fully developed at anthesis (gynoecium pseudomonomerous), although the two sterile carpels participate in the style and end in two (slightly smaller) stigmas. It contains a single (hemi)anatropous basal ovule. The flower is thus pronouncedly monosymmetric, with the fertile carpel in the median plane.

At anthesis, the two (slightly smaller) stigmas flanking the median stigma are positioned closer to the median stigma than to each other, and thus the three stigmas appear almost collateral. They are all broad, with a shallow median furrow on the ventral surface, and are reflexed toward the style. They are covered by uniseriate, multicellular papillae and may be slightly secretory (fig. 3*E*). At the transition from the stigmas to the style, the two sterile carpels unite first with the fertile carpel, and a short compitum appears to be present (figs. 3*D*, 4*C*). Further down, they also unite with each other and form a synascidiate (for term, see Endress 1994) style (fig. 4*E*–4*H*). The base of the stylar canal appears as a median slit in the ceiling of the locule (fig. 4*I*). The style is constricted by an abscission zone, where the upper part later abscises (fig. 3*A*). The gynoecium is of angiospermy type 4 (for term, see Endress and Igersheim 2000).

A distinctive pollen tube transmitting tract (PTTT) begins in the stigma and extends downward along the ventral slit of each carpel. The PTTT of the fertile (median) carpel is wider than those of the two sterile (lateral) ones. The three PTTTs are separate from each other in most of the length of the style (fig. 4*D*–4*G*). In the style's lowermost part, immediately above the ceiling of the locule, the PTTTs may become contiguous and

thus may form a short compitum only in its lowermost part, although the inner morphological surfaces of the two reduced carpels do not merge with that of the fertile carpel because of their ascidiate structure, and they cease at the base of the style (fig. 4*H*, 4*I*).

Each floral vascular bundle encloses a resin canal on the dorsal side of the xylem. In the style, the resin canals vanish for a short distance in a region that corresponds to the abscission zone, but they reappear further up (fig. 4*F*). Above the abscission zone, there is also a split of the median dorsal vascular bundle of each carpel into two branches, which extend along the stigmatic ventral furrow (fig. 4*B*–4*E*).

Thus, each stigma has two dorsal vascular bundles and four (or up to 12) laterals (fig. 4*B*). In addition, the vasculature of the flower remains independent from that of the involucre in the "fused" parts until it reaches the base of the ovary (fig. 4*G′*–4*O′*).

The dorsal vascular bundle of the fertile (median) carpel extends downward on the adaxial (narrow) side of the flower, whereas the dorsal vascular bundles of the two other (sterile) carpels extend downward on the abaxial side. Lateral bundles are arranged in series between the median dorsal vascular bundles of the three carpels. Together, they form a dense network, but a constant pattern was not noticed.

Floral development begins with the formation of a first carpel, with its ventral slit facing the floral-subtending bract. Later, two additional carpels appear on each edge of the ventral slit of the median and now larger first carpel (fig. 5). The locules of the two delayed (lateral) carpels do not develop further. Only the median carpel develops a locule and an ovule. As a result of the unequal growth of the carpels, the former center of the floral apex is lifted, together with the sterile carpels, to the stylar region close to the ventral slit of the fertile (median) carpel.

Another unusual feature is the position of the ovary. It is superior in the transverse plane but inferior in the median plane. This situation arises during development of the involucre, in which the narrower (median) sides of the ovary have been drawn upward by intercalary growth of the walls of the involucre, whereas such growth does not take place in the transverse plane. The median sides can also be described as incorporated or congenitally fused with the walls of the involucre.

Ovule of Amphipterygium

At anthesis, the single (hemi)anatropous, syntropous (for term, see Endress 1994) ovule ascends from the center of the base of the locule. It is crassinucellar and has a single integument. The micropyle is closed by lobes of different size and forms an irregularly shaped slit (fig. 6). Although the nucellus is almost horizontal, the micropyle is directed obliquely downward, toward the placenta. Unlike in almost all other angiosperms, the region between the placenta and the ovule is much larger than the ovule itself. It may be interpreted as a long and massive funicle (see "Discussion") with unusual outgrowths. The whole structure (ovule and funicle) fills the locule and is flattened in the plane of symmetry of the flower. It is thus pronouncedly monosymmetric. Its largest extension in transverse section is ca. 1.5 mm.

The funicle is folded in such a way that the shape of the whole structure is reminiscent of a sleeping duck, with its "head" turned backward and resting on its "back," whereby the ovule forms the head and the funicle the other parts of the body (fig. 6). The topographically uppermost part of the funicle, corresponding to the "neck," is tightly appressed to the dorsal side of the ceiling of the locule (fig. 4*A*) and is thus in direct contact with the PTTT coming down from the stigmas. A corresponding area was described earlier in *Mangifera* (Anacardiaceae) and called "ponticulus" (Joel and Eisenstein 1980). The lower part of the funicle also forms a median outgrowth that develops on the side opposite of the part that leads to the ovule and may be seen as the "tail" of the duck. Lateral outgrowths on the upper and lower parts of the funicle are here referred to as "upper wings" and "lower wings," respectively.

In median longitudinal section, the micropyle lies close to the back of the massive lower part of the funicle (fig. 6). The integument completely covers the nucellus on the convex side of the ovule, while it is extremely short on the concave side (as usual in a bitegmic anatropous ovule). In the micropylar region, there is a gap between the integument and the nucellus (fig. 6*A*–6*D*).

In contrast to the other vascular bundles of the gynoecium, the ovular vascular bundle is not associated with a resin canal and is surrounded by a tanniferous layer of elongated cells. It runs along the convex side of the funicle and ovule, from the placenta to the chalaza, where it splits into a few short branches, which, however, do not extend further into the integument. Vasculature is also lacking in the median appendage of the funicle. The subepidermal parenchyma on the convex side of the funicular vascular bundle shows three or four cell rows as a result of the excessive thickening of the funicle (including tail formation), and a loose parenchyma forms the massive lower part of the funicle on the concave side.

The ovule rises from the ventral base of the locule soon after initiation of the three carpels. When the floral base begins to be taken upward by the growth of the involucre, the funicle begins to bend and the integument to develop. While the ovary enlarges, the initial basal ventral insertion of the ovule changes to a more central position at anthesis, and the upper part of the bent funicle lies on the lower one. The development of the parenchyma up to anthesis is more pronounced on the concave side of the lower part of the funicle (fig. 6*A*–6*D*). Its upper part is pulled up and appressed toward the ceiling of the locule, especially its topographically uppermost region, thus forming a ponticulus (see "Discussion"), where the stylar canal enters the ovary (fig. 4*A*).

After anthesis, the parenchyma becomes even larger celled, with larger intercellular spaces (fig. 6*I*). While the ovary begins to develop into a fruit, the ovule-funicle complex still fills the locule. Near the zone of the bend of the funicle, two flattened lateral outgrowths sometimes develop out of the upper part of the funicle and may be seen as two small upper wings of the duck. These outgrowths develop downward and for a short distance cover the lower part of the funicle, which now represents four-fifths of the whole ovule-funicle complex. Lower wings develop as longitudinal lateral ridges on the lower part of the funicle. The median appendage of the funicle bends upward and toward the ovule and eventually partially covers it (fig. 6). Much later, a curved embryo with a massive hypocotyl

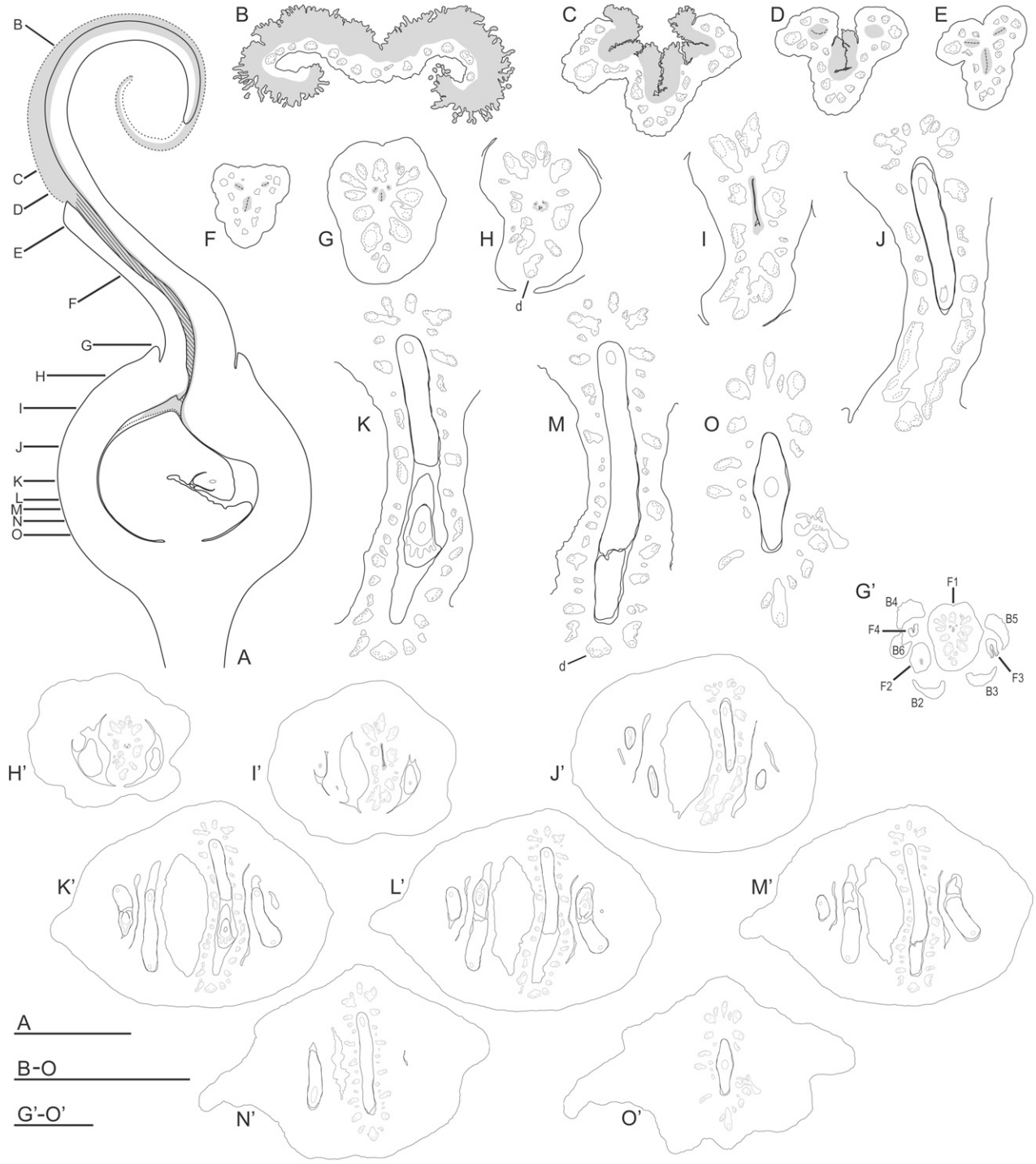

Fig. 4 *Amphipteryigum adstringens*. Anthetic female flower and samaroid unit. Morphological surfaces drawn with solid line, except for postgenitally fused surfaces, which are drawn with dashed lines in transverse section (TS); pollen tube transmitting tissue (PTTT) is shaded gray; median dorsal vascular bundle of fertile carpel marked with *d* in a few images. Scale bars = 1 mm. *A*, Schematic median longitudinal section (LS) of anthetic flower (*F1*) and samaroid unit. Parts just out of the median plane of symmetry are drawn with dotted lines; postgenitally fused areas are hatched. *B–O*, TS series of anthetic female flower (*F1*), *L* and *N* not shown. *B*, Stigma. *C*, Upper part of the style, incompletely united carpels, with short (external) compitum. *D*, Transitional region of the style, with ascidiate zone of sterile carpels and plicate zone of median fertile carpel. *E–H*, Synascidiate zone of the style. *F*, Style at level of abscission zone, where resin canals are not developed in the vascular bundles. *G*, Style below abscission zone. *H*, Base of the style with potential short (internal) compitum formed by the three contiguous PTTTs. *I*, Transitional zone between style and ovary with extended stylar canal. *J*, *K*, *M*, *O*, Locule with ovule. *G′–O′*, TS series of a samaroid unit (left pattern), corresponding to *G–O* and including *L′* and *N′*; vasculature drawn only for F1 (thin solid line) and lumen of resin canal (thin dashed line). *G′*, Four styles (*F1* has the largest) surrounded by five bracts (*B2–B6*). F1–F4 are indicated. *H′*, Narrow circular aperture on top of the involucre

and two flattened cotyledons develops in the seed. In the sterile flowers (F2–F4), the ovule does not develop into a seed but turns into a lacunar parenchymatic structure with a tanniferous periphery. In two sterile flowers, we observed ovules with traces of a second (outer) integument on the convex side.

Male Inflorescence and Flower of Amphipterygium

The lax male inflorescences form a compound thyrsoid with up to five orders of branching. Each flower has a subtending bract and two lateral prophylls. Lateral cymose branching is more frequent in the proximal part of the thyrsoid, with cymes of up to seven flowers. In the distal part of inflorescence axes of the first, second, and third orders, the uppermost lateral flower is sometimes connate with the terminal flower.

Each male flower comprises a single whorl of four to six (or seven) stamens, which alternate with as many sepals of about the same length. The sepals are united at the base and may be of irregular shape (fig. 7*A*, 7*B*).

The male structures are covered by hairs similar to those described for the female reproductive structures. Long unicellular to uniseriate multicellular hairs are present on the inflorescence axes and most floral organs, are lacking only on the stamen filaments, and are scarce on the ventral side of the sepals. Glandular hairs occur on the lower dorsal side of the sepals and the pedicel (fig. 7*A*–7*C*).

The outer epidermis of the sepals is thicker and contains more tannins than the inner one. The anthers are X shaped and basifixed to slightly ventrifixed. The ventral pollen sacs are slightly smaller and shorter than the dorsal ones. At the base of the anthers, the longitudinal dehiscence line curves toward the ventral side. The two thecae are free in the lower and upper quarters of their length (fig. 7*C*–7*G*). The thecae have a papillate epidermis and a conspicuous one-cell-layered endothecium. Each sepal has a main median vascular bundle (and sometimes one or two laterals), which comprises a resin canal and a ventral xylem. In contrast, the vascular bundle of the stamen lacks a resin canal.

Pollen grains are spherical and have more than three small, roundish apertures (up to 12, according to Erdtman 1952). The ectexine is microreticulate, and the muri have a verrucate and irregularly vermiculate ornamentation (fig. 7*H*–7*J*).

Female Inflorescence of Pistacia

In *Pistacia lentiscus*, inflorescences are produced in the axils of persistent foliage leaves that developed in the previous year, mostly in the distal region of the shoot. They comprise two (sometimes three or four) lateral botryoids (for term, see Weberling 1989) of alternate, more or less sessile flowers (sometimes compound botryoids, with a terminal and few basal lateral botryoids). The botryoids are clustered on a short axis, which ends in an undifferentiated bud protected by five or six cataphylls. This bud may develop into a vegetative shoot after flowering, with infructescences at the base and new inflorescences formed in the distal region. On the maturing fruit, remains of dried style and stigmas are persistent. Glandular hairs with a uniseriate stalk and a multicellular head are sparsely present on the inflorescence axes. Inflorescences of other species studied are also (compound) botryoids (*Pistacia mexicana*) or (compound) thyrsoids (*Pistacia atlantica*, *Pistacia terebinthus*, *Pistacia vera*), with some variation in the branching orders.

Female Flower of Pistacia

The description of the structure and development of the female flower and ovule is based on *P. lentiscus* (figs. 8–10). Observed variations for the four other species studied are indicated if of interest. Each flower has a subtending bract. It consists of a tricarpellate gynoecium, which is surrounded by five (to eight) sepal-like organs. If five are present, they have a quincuncial aestivation (fig. 10*A*, 10*B*). Whether they are sepals or bracts is not clear (see "Discussion"). In *P. terebinthus*, five (to 10) sepal-like organs were found, but in *P. mexicana*, only two were found. Occasionally, we found reduced stamens (*P. lentiscus*; this study) or stamen primordia that do not further develop (*P. vera*; Hormaza and Polito 1996) (fig. 8*B*, 8*C*).

The gynoecium comprises a superior subglobular ovary and a short style ending in three bilobed stigmas. The ovary is unilocular, as only one of the three carpels is fully developed at anthesis (gynoecium psueudomonomerous), although the two sterile carpels participate in the style and form two (slightly smaller) stigmas (fig. 8*D*). It contains a single anatropous, basal ovule (fig. 9*A*). As a result, the gynoecium is monosymmetric, with the fertile carpel in the symmetry plane (fig. 9). However, the floral symmetry plane is oblique with regard to the inflorescence axis in all species studied, and no fixed pattern was found.

At anthesis, the three stigmas are arranged more or less radially (fig. 8*D*). They have a shallow median furrow on the ventral side and are more or less reflexed (fig. 9*A*–9*C*). They are covered by uniseriate, multicellular secretory papillae (fig. 8*E*). At the transition from the stigmas to the style, the two sterile carpels unite first with the fertile carpel, and there appears to be a short compitum (for term, see Endress 1994) (fig. 8*D*). Further down, they also unite with each other. The style is synascidiate, at least in its lower part (fig. 9*G*, 9*H*); it lacks an abscission zone. The unilocular (pseudomonomerous) ovary contains a single basal anatropous ovule (fig. 9*J*–9*M*). A median slit in the ceiling of the locule represents the lower end of the stylar canal (fig. 9*I*). The gynoecium is of angiospermy type 4 (for term, see Endress and Igersheim 2000).

In *P. lentiscus*, as well as in other species studied, at anthesis, the stigmas are flat or more or less reflexed toward the

(cupule), through which the styles are exserted. The narrow sides of the ovary of F1 are fused on both sides with the involucre (cupule); F4 is fused on one side; the other two flowers are still free at this level. *I′*, Narrow sides of the ovary of F2 are also fused with the involucre (cupule). *J′*, Four collateral flowers are spaced by lacunae that look like slits. The large width of the lacuna between F1 and F2 is an artifact. *K′*, Ovules with same orientation in F1 and F4. *L′*, Ovules with same orientation in F2 and F3. *M′*, Ovules in F1, F2, and F3 with tail. *N′*, F1 flanked by two lacunae and F2 on the left. F3 and F4 fused with involucre (cupule). *O′*, F1 with the base of the ovary embedded in the base of the involucre and its vasculature beginning to merge with that of the involucre.

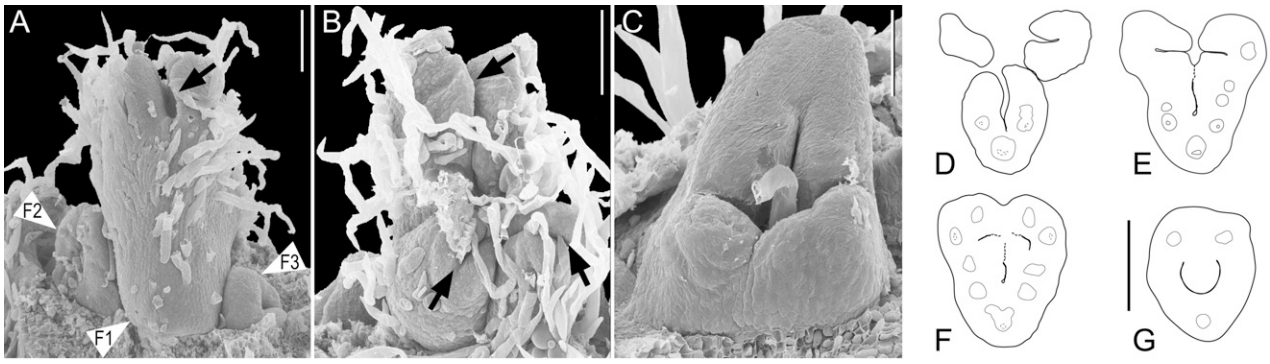

Fig. 5 *Amphipterygium adstringens*. Young samaroid unit and female flowers. Black arrows point to ventral slits of carpels; white arrowheads point to flowers. Scale bars: *A*, *B* = 0.1 mm; *C* = 60 μm; *D*–*G* = 0.2 mm. *A*, Samaroid unit (left pattern), from adaxial side. Only the median fertile carpel of F1 is visible, from its dorsal side. All bracts of the involucre removed. *B*, Same F1, from the opposite side. The ventral slits of its three carpels are visible. *C*, Flower (*F2*) with its three carpels of a samaroid unit older than that in *A*, *B*. *D*–*G*, Transverse section series of flower (*F1*) of the very young (preanthetic) samaroid unit shown in fig. 2*E*, 2*F*. *D*, Future plicate stigmatic region. *E*, Upper style, partially symplicate. *F*, Lower style, synascidiate. *G*, Locule with young ovule.

style. In *P. mexicana* and *P. vera*, the floral subtending bract and the first two lateral organs in transverse position are longer than the style and stigmas.

A distinctive PTTT begins in the stigma and extends downward along the ventral slit of each carpel. The PTTT of the fertile carpel is wider than those of the two lateral ones. The three PTTTs remain separate from each other, as the style is synascidiate (fig. 9*G*, 9*H*). Those of the reduced carpels cease toward the base of the style, while that of the fertile carpel continues toward the ceiling of the locule (fig. 9*I*). The vasculature of the gynoecium is variously differentiated at anthesis, although each vascular bundle later encloses a resin canal with a ventral xylem.

At anthesis, the dorsal vascular bundle of each carpel may split into two branches, which extend along the ventral furrow of each stigma (as observed in *P. vera*) (fig. 9*B*). Further down in the style, the dorsal bundle may be less differentiated than the lateral vascular bundles, but it becomes more distinct again toward the base of the style, before the ovary starts. The dorsal vascular bundle of the median fertile carpel can be traced downward to the base of the ovary, whereas that of the sterile carpels is less distinct in the ovary and forms a dense network with lateral traces. Although no constant pattern is apparent, there is often a median ventral vascular trace. It may be interpreted either as the median ventral vascular bundle of the fertile locule or as a synlateral vascular bundle formed by the lateral vascular traces of the sterile carpels. Lateral traces are arranged in series in the ovary wall, around the locule.

Uniseriate hairs are found mostly on the margins of the sepal-like organs. Glandular hairs with a uniseriate stalk and a multicellular head are sparsely present at the basal ventral surface of the sepal-like organs.

Floral development begins with the initiation of the five (to eight) sepal-like organs. They attain a quincuncial aestivation, with the first two in transverse position (fig. 10*A*, 10*B*). One to three additional, smaller organs may also be formed; they appear to represent staminodes, as they may show rudimentary pollen sacs.

Early in gynoecium development, one of the three carpels becomes larger. The formation of a first, off-centered depression corresponds to the incipient locule of the fertile carpel. Later, two additional depressions, corresponding to the locules of the two sterile carpels, appear more or less simultaneously on the side opposite the fertile carpel (see also Marchand 1869) (fig. 10*C*). A mound representing the future ovule then forms on the ventral side of the fertile carpel, which is still widely open, and the former center of the floral apex between the three locules is still visible. The two sterile locules do not enlarge further (fig. 10*D*). While the ovule develops, growth of the lateral and ventral sides of the fertile carpel closes the locule and forms the median slit in the ceiling, corresponding to the lower end of the stylar canal (fig. 10*E*–10*H*). As a result of unequal growth of the carpels, the former center of the floral apex is lifted, together with the sterile carpels, to the stylar region. The development of the two sterile carpels is variable in the genus. Their aborted locules, though not communicating with the fertile locule, remain as closed, narrow canals in the style or, as occasionally observed in *P. mexicana*, extend downward along the ventral wall of the ovary for some distance.

Ovule of Pistacia

In *P. lentiscus*, at anthesis, the single crassinucellar, unitegmic, (hemi)anatropous, and syntropous (for term, see Endress 1994) ovule ascends from the ventral base of the fertile locule. A micropyle is not formed at anthesis, as the integument does not close, and the nucellus is broadly exposed. The nucellus tip is directed downward and is in contact with the floor of the locule (fig. 11*A*, 11*E*).

The region between the ovule proper and the placenta is formed by an extensive funicle. The entire structure (ovule and funicle) fills the locule, its plane of symmetry matching that of the flower. Its largest extension in transverse section is ca. 0.38 mm. The funicle is bent at about midlength. Its topographically uppermost part forms a shallow crest (ponticulus) (see "Discussion"), which extends into the median cleft (stylar canal) in the ceiling of the locule and is tightly appressed to it (fig. 9*A*; fig. 11*E*, 11*K*). The funicle has a small median outgrowth on the side opposite the one that leads to the ovule.

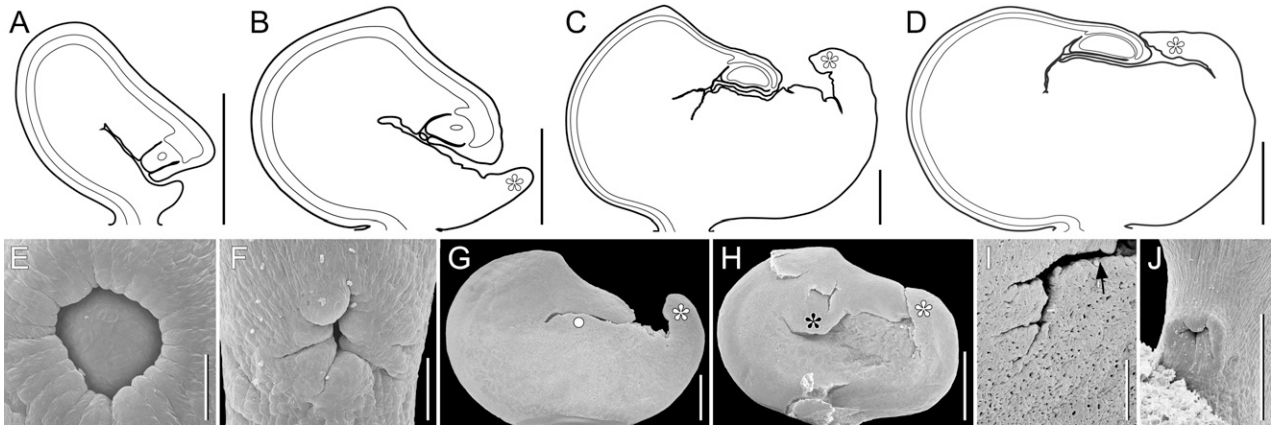

Fig. 6 *Amphipterygium adstringens*. Ovules and funicles. Scale bars: *A*, *I*, *J* = 0.3 mm; *B* = 0.5 mm; *C*, *D*, *G*, *H* = 1 mm; *E* = 40 μm; *F* = 60 μm. *A–D*, Ovule and funicle development, schematic median longitudinal section. *A*, *B*, Two ovules from the same samaroid unit with anthetic F1. *A*, Ovule of F4. *B*, Ovule of anthetic F1. The ovule begins to look like a sleeping duck. The lower part of the funicle represents the "body" and the ovule the "head." *C*, Ovule of postanthetic F1. The "tail" (asterisk) is bent backward, toward the head (ovule). *D*, Ovule of postanthetic F1 still older than that in *C*. The tail (asterisk) partly covers the head (ovule). *E*, *F*, Close-up of micropyles of two different ovules from the same anthetic samaroid unit. *E*, Unclosed micropyle of the ovule of F4 (corresponding to *A*). *F*, Micropyle closed by thick lobes of the ovule of the anthetic F1 (corresponding to *B*). *G*, Ovule of a postanthetic F1 (corresponding to *C*); tail marked with asterisk, "lower wing" with dot. *H*, Ovule of a postanthetic F2; tail marked with white asterisk, "upper wing" with black asterisk. *I*, Close-up of the region of the funicular bend of an ovule of the same stage as *C* and *G*. Note the spongy aspect of the funicle. Arrow points to micropyle. *J*, Close-up of micropyle of an ovule of a postanthetic F1 (corresponding to *D*).

In *P. vera* and *P. mexicana*, the dorsal crest of the funicle is usually more papillate than the adjacent area (fig. 11*N*–11*P*). In *P. mexicana*, the median outgrowth is almost absent, and the nucellus tip is directed more toward the base of the funicle than toward the floor of the locule. *Pistacia vera* has a distinct outer integument in the convex half of ovule curvature (fig. 11*M*, 11*N*).

In *P. lentiscus*, the integument does not close at the nucellus apex; thus, there is no micropyle at anthesis. It is slightly thicker and longer on the convex side of the ovule than on the concave side. The ovular vascular bundle does not contain a resin canal, in contrast to the other vascular bundles of the gynoecium. It runs from the placenta along the convex side of the funicle to the chalaza (fig. 11*A*–11*D*).

The ovule is initiated at the ventral base of the fertile locule when the syncarpous ovary begins to develop. The ovule (including funicle) fills the locule during floral development, matching the growth of the locule up to anthesis (fig. 9*A*).

However, during the first postanthetic phase, the whole structure (funicle and ovule) grows more slowly and does not fill the locule for some time. The successive development of outgrowths of the funicle will confer on the whole complex a shape reminiscent of that of a swan pulling its "head" backward between its "wings," whereby the ovule is seen as the head and the funicle as the other parts of the body (fig. 11). The lower part of the funicle, which arises from the placenta, considerably enlarges. As a result, the entire structure (funicle and ovule) is tilted, and its insertion in the locule appears more central than at anthesis. The lower part of the funicle now forms the bulk of the body, with a well-developed "tail" flanked by two additional basal lateral outgrowths, the "lower wings" (fig. 11).

The topographically upper part of the funicle, which comprises the ovule, is raised by the growth of the lower part. The micropyle is now almost closed by the short-lobed integument. A gap remains between the nucellus and the integument in the micropylar region. The nucellus is now directed more horizontally (fig. 11*C*, 11*D*, 11*G*, 11*H*).

Two lateral flattened outgrowths develop from the upper part of the funicle, near the zone of the bend, the "upper wings." They develop downward and tend to embrace the base of the funicle, whereas the tail and the lower wings develop upward and tend to cover the head (fig. 11*I*–11*K*). Once all outgrowths are well developed, the whole ovule-nucellus complex further enlarges and progressively fills the locule. The expansion of the funicle appears to be due mainly to cell growth and increase in size of intercellular spaces (fig. 11*Q*, 11*R*).

In contrast to other *Pistacia* species studied (fig. 11*M*, 11*O*, 11*R*), in *P. mexicana*, lower wings do not develop, and upper wings remain small (fig. 11*P*). However, there is a proliferation of bumpy parenchymatous tissue in the upper region of the funicle, in the area of the former ponticulus. Thus, in this species, the ovule-funicle complex resembles a question mark rather than a bird.

Male Inflorescence and Flower of Pistacia

Each inflorescence comprises two (sometimes three or four) botryoids, developing in the axil of a bract on a short axis that ends in a vegetative bud protected by five or six spirally arranged cataphylls. Each flower develops in the axil of a bract and has four to six (usually five) sepals (bracts?) and the same number of stamens. The sepals (bracts?) are spirally arranged (quincuncial aestivation when five are present); the two outermost organs are in transverse position. Each stamen is basally fused with a sepal (bract?). A tricarpellate sterile gynoecium is also present, comprising a larger carpel that encloses an aborted ovule (fig. 12*A*, 12*B*).

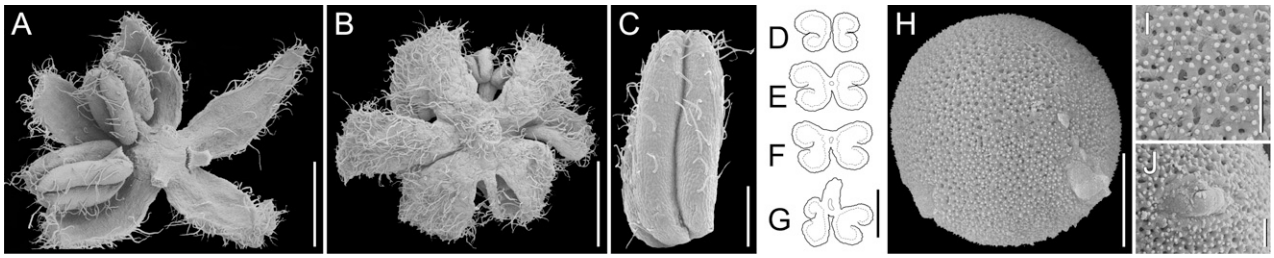

Fig. 7 *Amphipterygium adstringens*. Male flowers and pollen. Scale bars: *A*, *B* = 0.8 mm; *C* = 0.25 mm; *D*–*G* = 0.2 mm; *H* = 9 μm; *I*, *J* = 2 μm. *A*, *B*, Male flowers. *A*, From above, showing five stamens (three anthers removed) alternating with five sepals. *B*, From below, showing five sepals briefly united. Between the two lower sepals, there is a sixth, narrow organ, perhaps a reduced sepal. *C*–*G*, Anthers. *C*, From lateral, ventral side at right, showing the dehiscence slit. *D*–*G*, Transverse section series, ventral side up. *D*, Free upper parts of the two thecae. *E*, At midlength, showing the latrorse dehiscence and the more or less central position of the thin connective. *F*, Toward the base, showing the slightly ventral position of the connective. *G*, At the base, dorsal pollen sacs longer than the ventral ones, transition to the filament. *H*–*J*, Pollen. *H*, Entire pollen grain. *I*, Extra-apertural ectexine. *J*, Protruding aperture.

The anthers are almost basifixed, slightly ventrifixed, and introrse. Their dorsal pollen sacs are broader and longer than the ventral ones. They extend further down than the connective insertion, and they apically overarch the ventral thecae. The longitudinal dehiscence line of the anther consequently curves toward the ventral face of the stamens in both the lower and higher part of the thecae (fig. 12*C*–12*G*).

The connective is relatively massive, with broad vascular supply. The epidermis is papillate, and the endothecium cells are larger in the dorsal region of the anthers than in the ventral.

Pollen grains are spherical and have more than three small, irregularly roundish apertures, with irregularly sculptured exine. The ectexine is microreticulate, and the muri have a verrucate ornamentation (fig. 12*H*–12*J*).

Discussion

Morphological Interpretation of the Samaroid Unit of Amphipterygium *and Comparison with Cupules of Other Rosids*

Our developmental study shows that the branching pattern of the samaroid unit in *Amphipterygium* is a cyme with a primary dichasial (flowers F1–F3) and further monochasial branching (flowers F4 and F5). This pattern has not been recognized before. Earlier authors did not even address the branching pattern.

The involucre, or cupule, is formed by the union of the bases of five bracts, on the rim of a few-flowered capitulum. Their growth up to the base of the styles of the collateral pistillate flowers before anthesis results in the almost closed and cup-shaped end of the samaroid unit. There is a tight coordination between the development of the bracts and the successive initiation of flowers. According to their position and sequence of initiation, the subtending bract of the samaroid unit (B1) is also the subtending bract of flower F1, and B2 and B3 are the prophylls of F1 and at the same time the subtending bracts of F2 and F3. The two subsequent bracts, B4 and B5, are initiated before F2 and F3, and they are each one of the two prophylls of F2 and F3. Likewise, B4 is the subtending bract of F4. B5 usually has no flower in its axil. Between B4 and B2, B6 develops and is one of the two prophylls of F4. The five teeth on top of the involucre, which were originally described by Schlechtendal (1843*b*) but without an interpretation of their morphological significance, are the free ends of the five bracts B2–B6 (fig. 2*H*).

Cupules are conspicuous elaborations of a number of rosid families. They are sturdy envelopes protecting fruits, commonly nuts with a starchy seed, and they may be morphologically complex.

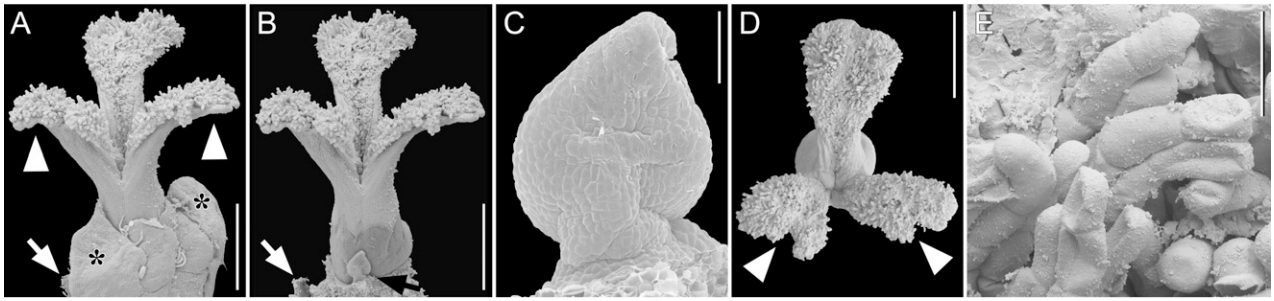

Fig. 8 *Pistacia lentiscus*. Anthetic female flowers. White arrow points to floral subtending bract; arrowheads point to stigmas of the sterile carpels. Scale bars: *A*, *B*, *D* = 0.5 mm; *C* = 50 μm; *E* = 40 μm. *A*, Female flower, from lateral view. Asterisks indicate the two sepals (bracts?) in transverse position. *B*, Same flower, all sepals (bracts?) removed. Black arrow points to a staminode at the base of the ovary. *C*, Close-up of the staminode shown in *B*. *D*, Same flower, all sepals (bracts?) removed, from above. Note the two smaller (sterile) bilobed stigmas, arranged radially. *E*, Same flower, close-up of the multicellular stigmatic papillae.

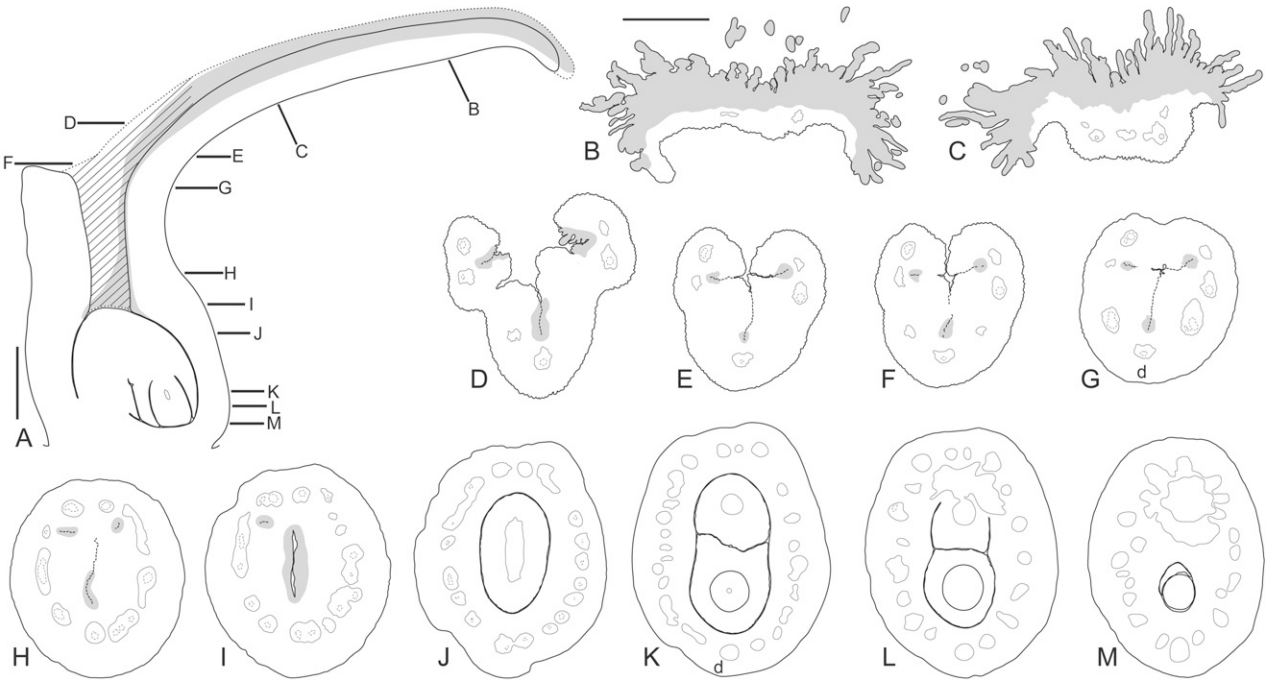

Fig. 9 *Pistacia lentiscus*. Anthetic female flower. Morphological surfaces drawn with solid line, except for postgenitally fused surfaces, which are drawn with dashed lines in transverse section (TS); pollen tube transmitting tissue (PTTT) shaded gray; median dorsal vascular bundle of the fertile carpel marked with *d* in a few images. Scale bars = 0.2 mm. *A*, Schematic median longitudinal section of gynoecium of anthetic flower. Parts just out of the median plane of symmetry are drawn with dotted lines; postgenitally fused areas are hatched. *B–M*, TS series of anthetic flower. *B*, *C*, Stigma of fertile carpel. *D–F*, Upper part of the style, incompletely united carpels. *F*, *G*, Transitional region of the style, with ascidiate zone of the sterile carpels on the left side and plicate zone of the sterile carpel on the right side, and the median fertile carpel. *H*, Synascidiate zone of the style. *I*, Transitional zone between the style and ovary with extended stylar canal. Note that at this level, only the inner surface of the sterile carpel on the left side is still present. *J–M*, Locule with ovule.

A shared pattern is a compressed system of one or several branching orders, including bracts, that form a "coenosome," a compact structure of more or less strongly united structural units. However, comparative developmental studies have shown that their morphological constitution is diverse and varies from family to family where cupules occur. In *Amphipterygium*, the cupule is a cyme with three or four branching orders in which all branches but one or two end in a flower (this study) (fig. 2*G*). A few other Anacardiaceae show incipient cupules of less compacted branches that are easier to analyze but with the same general structure (*Blepharocarya*, *Laurophyllus*; Wannan et al. 1987; Wannan and Quinn 1992). In Fagaceae (Fagales), the cupule is also a cyme but with numerous branching orders and only the first one, two, or three ending in a flower (Fey and Endress 1983; Rozefelds and Drinnan 2002). In Myricaceae (Fagales), the structure is similar, but there are fewer branching orders, and the cupule is completely united with the fruit that terminates the first branching order (Macdonald 1979, 1980). In Balanopaceae (Malphigiales), the cupule structure is simpler and consists of crowded bracts of a single branching order (Merino Sutter and Endress 2003). The nonhomology between these different cupules indicates their separate evolutionary origin and is in agreement with the findings that these families are only remotely related within rosids (APG 2003).

A cupule containing several flowers but forming a closed indehiscent dispersal unit is a unique combination of features and therefore was originally used to erect the Julianiaceae. Within Anacardiaceae, there are a number of other genera with samaroid (winged) diaspores, but they are morphologically different and more simple and are derived from single flowers and not from (partial) inflorescences (*Blepharocarya*, *Cardenasiodendron*, *Dobinea*, *Faguetia*, *Loxopterygium*, *Pseudosmodingium*, *Schinopsis*, and *Smodingium*; Pell 2004).

Within Anacardiaceae, *Orthopterygium* and *Amphipterygium* form a well-supported clade (*trn*L-F; 99% bootstrap support) nested in Anacardioideae (Pell 2004), and thus, the peculiar cupulate samaroid units of both former Julianiaceae are likely homologous. The samaroid units of *Orthopterygium* are more symmetrical than those of *Amphipterygium* because in *Orthopterygium*, they contain only three flowers (Hemsley 1906, 1907) (apparently in a dichasium), whereas in *Amphipterygium*, they contain four flowers, with an additional monochasial branching on one side of the dichasium. As a consequence, in *Amphipterygium*, the side on which even-numbered flowers (F2 and F4) and their subtending bracts (B2, B4, and B6) develop becomes more convex than the side with the odd numbers (fig. 2*B*, 2*C*). The three flowers that develop in the samaroid units of *Orthopteygium* appear to correspond to F1, F2, and F3 in *Amphipterygium*.

Female Flowers

The female flowers of *Amphipterygium* and *Pistacia* lack petals, and the syncarpous gynoecium is tricarpellate. The two

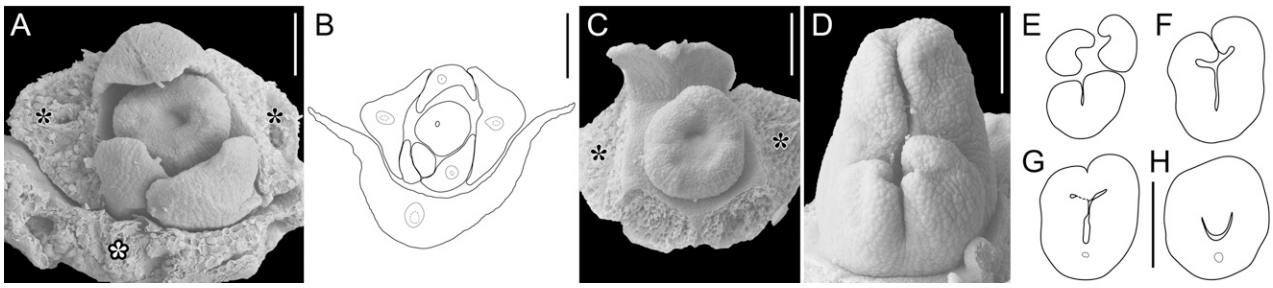

Fig. 10 *Pistacia lentiscus*. Young female flowers. White asterisk indicates the position of the floral subtending bract, black asterisks indicates the two sepals (bracts?) in transverse position. Scale bars: *A*, *C*, *D* = 0.1 mm; *B*, *E–H* = 0.2 mm. *A*, Young preanthetic flower, from above. Floral bract and two sepals removed to show the quincuncial aestivation. *B*, Transverse section (TS) of young preanthetic flower older than that in *A*. Note the (quincuncial) cochlear aestivation and the presence of a sixth organ (staminode). *C*, Young preanthetic flower (stage corresponding to *A*), from above. Floral bract and four sepals (bracts?) removed to show the three incipients locules. *D*, Young preanthetic gynoecium (stage corresponding to *B*), from lateral. *E–H*, TS series of young preanthetic gynoecium, older than that in *D*. *E*, Future plicate stigmatic region. *F*, Short upper stylar region. *G*, Transitional zone, from symplicate to synascidiate. *H*, Locule with young ovule.

to 10 (usually five) sepal-like organs in *Pistacia* were interpreted as bracts by Marchand (1869) and Zohary (1952) but without convincing evidence, apart from an irregular number, variable size, and different attachment levels. The presence of quincuncial aestivation (fig. 10*A*, 10*B*), if five organs are present (not mentioned by these authors), would fit with a sepaline nature but is not enough support for it. If the interpretation of the flowers as asepalous is correct, both *Amphipterygium* and *Pistacia* would have completely perianthless female flowers. However, we do not deal with this question here, as it needs comparison with more genera within the family.

The gynoecium has a unilocular ovary with a synascidiate style ending in three stigmas, which represent the tips of the three carpels, whereas the lower parts of two carpels are highly reduced and sterile. The unequal development of the carpels in the ovary makes it difficult to use the common terminology to describe a syncarpous gynoecium (Leinfellner 1950; see also Endress 1994). The ovary contains a single (hemi)anatropous ovule, with a basal insertion. In early development, three incipient locules are distinct in both *Amphipterygium* (this study) and *Pistacia* (Payer 1857; Marchand 1869; Takeda et al. 1979; Martinez-Pallé and Herrero 1995; Hormaza and Polito 1996), but they stop growing early, and only one is fertile and fully developed at anthesis (Grundwag and Fahn 1969). The stigmas of the sterile carpels are regularly smaller than that of the fertile carpel (Payer 1857; Copeland 1955; Takeda et al. 1979; Martinez-Pallé and Herrero 1995; Hormaza and Polito 1996; Shuraki and Sedgley 1997) (fig. 8). Sometimes in *Pistacia*, only one (or none) of the two sterile carpels develops a stigma (Zohary 1952; Grundwag and Fahn 1969; Grundwag 1976; Hormaza and Polito 1996). More rarely, gynoecia with two or three locules and ovules are present in *Pistacia*, especially in *Pistacia lentiscus* (Grundwag 1976). In *Amphipterygium*, only F1 and maybe F2 are fertile (Schlechtendal 1843*b*; Hemsley 1901, 1906, 1907; Hemsley and Rose 1903), and F3 and F4 are abortive. However, they have (regularly, at least for F3) a unilocular ovary, a sterile ovule, a single stigma, and a single PTTT (this study) (fig. 4*G′–4O′*).

During development of the gynoecium, the reduced ovaries (locules) of the sterile carpels are lifted by the growth of the fertile carpel and then appear laterally at the base of its ventral slit. Concomitantly, the former center of the floral apex, initially located in the middle of the three carpels (see also Eckardt 1937; Endress 2006), is lifted and is finally situated close to the base of the ventral slit of the fertile carpel in the upper part of the style. The locule of the fertile carpel thus appears "ascidiate." However, its structure is more complex because it also encompasses the solid bases of the two reduced carpels. Where the three stigmas meet, above the style, they may form a short external compitum extending a short way downward into the style. A regular internal compitum is not formed in the style because the style is largely synascidiate. However, in *Amphipterygium*, neighboring PTTTs may become contiguous toward the base of the style (without a merger of the internal morphological surface of the carpels). Shuraki and Sedgley (1997) also mentioned this for *Pistacia vera* but without an analysis of the inner morphological surfaces.

In *Pistacia mexicana*, the inner surfaces and the PTTTs of the two reduced carpels may sometimes extend below the style, down to midlength of the ovary wall. In *P. vera*, pollen tubes can grow downward along the ventral side of the ovary to reach the base of the ovule (Shuraki and Sedgley 1997). However, it is unknown whether they follow the pathway of the PTTT of one or both of the reduced carpels.

Ovules

In *Amphipterygium* and *Pistacia*, the ovules and the complexes of ovule and funicle are extremely similar. The (hemi)anatropous ovule is unitegmic. The micropyle, topographically on the lower side of the ovule, is formed by the lobed integument and closes relatively late (at anthesis in *Amphipterygium* and after anthesis in *Pistacia*). The micropylar lobes are an architectural necessity for the closure of the originally circular opening (Igersheim and Endress 1997; Endress and Igersheim 2000). The integument is vascularized in the seed (Kühn 1928).

In both genera, the placenta is at the base of the locule, and the ovule is located on an extensive funicle. The funicle is bent in the direction of ovule curvature. The convex side of the

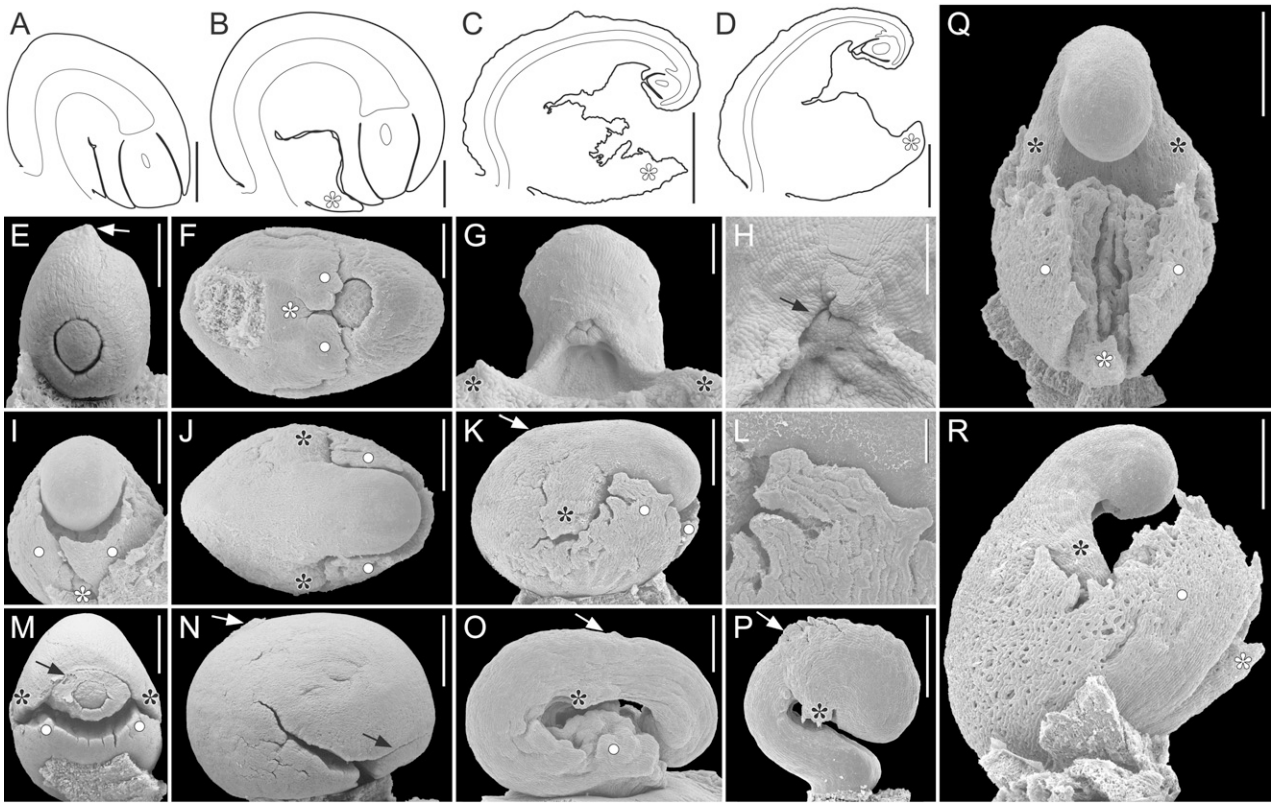

Fig. 11 *Pistacia*. Ovules and funicles. White arrows point to ponticulus when visible; white asterisks indicate the median basal outgrowth of the funicle corresponding to the "tail" of the "swan"; black asterisks indicate the median lateral appendages corresponding to the "wings." Scale bars: *A*, *B*, *E*, *F*, *L* = 0.1 mm; *C*, *D* = 1 mm; *G*, *H*, *M*, *N* = 0.2 mm; *I–K*, *O*, *P* = 0.4 mm; *Q*, *R* = 0.6 mm. *A–L*, *Pistacia lentiscus*. *A–D*, Ovule and funicle development, schematic median longitudinal section. *A*, Ovule of anthetic flower (collected April 22, 2005). *B–D*, Ovules of postanthetic flowers. *B*, Ovule, 1 mo after anthesis (collected May 24, 2004). The lower part of the funicle starts to increase in size and the ovule to tilt. *C*, Ovule corresponding to *Q*, *R* (collected August 23, 2004). The ovule looks like a swan, the lower part of the funicle representing the "body" and the ovule the "head." Note that the nucellus is now horizontal. *D*, Ovule, older than that in *C* (collected September 2, 2005). The funicle has greatly increased in size, and the swan starts to soar. *E–I*, Micropyles of four different ovules. *E*, Unclosed micropyle of ovule of anthetic flower (corresponding to *A*). Note the edge (arrow) on top of the funicle, which projects into the stylar canal and forms a ponticulus. *F–I*, Micropyles of ovules of postanthetic flowers. *F*, Micropyle still unclosed (corresponding to *B*). Note the development of the tail, flanked by two "lower wings." *G*, Micropyle almost closed (corresponding to *C*). *H*, Micropyle closed with irregular lobes (corresponding to *D*). *I–L*, Ovule and funicle of postanthetic flower (collected August 16, 2004), in different views. *I*, From the front. Note how the head of the swan (ovule) is fitting between the lower wings. *J*, From above, ovule at right. *K*, Lateral view, ovule at right. One of the "upper wings" and one of the lower wings flanking the tail (see *F*) are visible. *L*, Close-up of the lobes of a lower wing. *M*, *N*, *Pistacia vera*, ovule and funicle of an anthetic flower. *M*, From the front, showing the unclosed micropyle, the partial outer integument, and the lobed edges of the lower part of the funicle (lower wings). *N*, Lateral view, ovule at right. Note the edge (arrow) on top of the funicle, which projects into the stylar canal and forms a ponticulus. *O*, *Pistacia atlantica*, ovule and funicle of postanthetic flower. Note the massive lower part of the funicle, the ponticulus (arrow), and the small upper wing (asterisk). *P*, *Pistacia mexicana*, ovule and funicle of postanthetic flower. The lower part of the funicle is much less pronounced than in the other three species studied; in contrast, the region of the ponticulus is more conspicuous, and the upper wings (asterisk) are present. *Q*, *R*, *Pistacia lentiscus*, ovule and funicle of postanthetic flower (corresponding to *C*, *G*). *Q*, From the front, showing ovule, upper wings (black asterisks), and the folded structure and foamy aspect of the lower part of the funicle, comprising the tail (white asterisk) and the lower wings. *R*, Lateral view. The ovule looks like a soaring swan. The head (ovule) is rising from the body, and the tail and the upper and lower wings are visible.

bend follows the ventral side of the locule. The funicle has a lower (proximal) and an upper (distal) part. Interestingly, small differences in shape of the fertile ovule at anthesis between the two genera may be even smaller if such an ovule is compared with other developmental stages in the other genus. The (fertile) ovule of *Amphipterygium* plus funicle of an anthetic F1 is reminiscent of those of *Pistacia* after fertilization, especially those of *P. lentiscus*. In *Pistacia*, the direction of the ovule of an anthetic flower is like that of a (sterile) ovule of F4 in *Amphipterygium* (figs. 6, 11).

In both genera, the lower part of the funicle considerably increases between anthesis and onset of seed growth. Then, the funicle appears inflated and foamy, with large intercellular spaces. Its lower part has a pair of lateral appendages (lower wings) and a median appendage (tail), and its upper part has a pair of upper wings, giving the impression of a sleeping duck

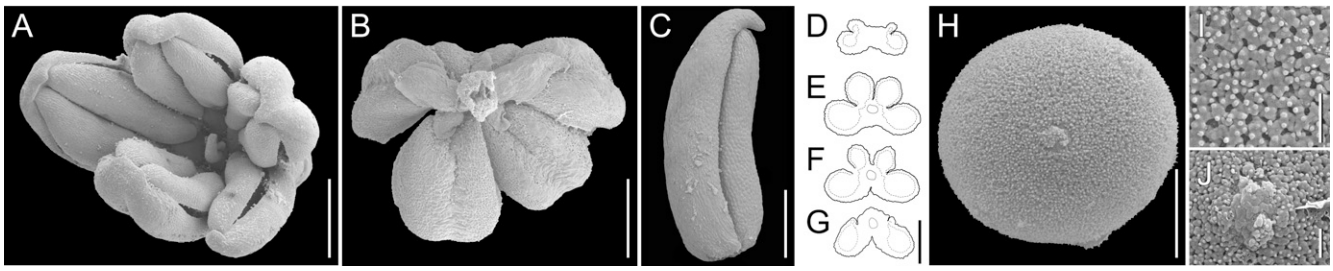

Fig. 12 *Pistacia lentiscus*. Male flowers and pollen. Scale bars: *A*, *B* = 0.8 mm; *C* = 0.5 mm; *D*–*G* = 0.2 mm; *H* = 9 μm; *I*, *J* = 2 μm. *A*, *B*, Male flowers. *A*, From above, showing five stamens and a central aborted gynoecium. *B*, Male flower, from below, showing five sepals (bracts?) and five stamens in the same radii and basally fused with the sepals (bracts?). *C*–*G*, Anthers. *C*, Lateral view, showing the dehiscence slit, ventral side at right. *D*–*G*, Transverse section series, ventral side up. *D*, Upper parts of the thecae. *E*, At midlength, showing introrse shape. *F*, Toward the base, showing the slightly ventral position of the connective. *G*, At the base, dorsal pollen sacs longer than ventral ones, transition to the filament. *H*–*J*, Pollen. *H*, Entire pollen grain. *I*, Extra-apertural ectexine. *J*, Protruding aperture.

(*Amphipterygium*) or swan (*Pistacia*), depending on slightly different proportions. Boodle (in Hemsley 1907) uses the term "funiculus appendiculatus" for *Amphipterygium* with regard to the tail. Copeland and Doyel (1940) interpreted this part as an obturator, based on the drawings of Boodle (in Hemsley 1907), because it is present at anthesis and adjacent to the ovule. However, it has not been shown that it plays a role in pollen tube guidance, and in *Pistacia*, it develops only after anthesis and is even lacking in *P. mexicana* (this study) (fig. 11*O*, 11*P*).

It has been suggested for *Pistacia* that the funicle appendages were transformations of a second integument (Grundwag 1976). We observed in both genera the occasional formation of a second integument on the outer side of the first integument on the convex side of ovule curvature, close to the micropyle, as reported in earlier studies for several species of *Pistacia* (Marchand 1869; Copeland 1955; Grundwag and Fahn 1969; Grundwag 1976; Shuraki and Sedgley 1997) (fig. 11*M*, 11*N*). This indicates that the commonly unitegmic condition in *Amphipterygium* and *Pistacia* originated from "fusion" of the two integuments present in other Anacardiaceae. Currently, this is what is also assumed for the origin of the thick single integument in *Anacardium* and *Mangifera* (Copeland 1961; Joel and Eisenstein 1980; Moncur and Wait 1986; de Wet et al. 1986). However, recent work on the mechanisms of derived unitegmy in *Impatiens* (Balsaminaceae) showed in *in situ* hybridization studies that developmental pathways may be variable (McAbee et al. 2005). This technique applied to *Pistacia* may be used to explain the origin of the appendages and whether they are linked to the reduction of the outer integument on the concave side of ovule curvature.

In both genera, the topographically upper part of the funicle is in close contact with the wall of the locule in the area of the apical cleft (figs. 4*A*, 9*A*); that it is a pathway for pollen tubes was first shown for *Toxicodendron* and *Pistacia* (Copeland 1955). Similar architecture and pathway for pollen tubes were later described in *Mangifera* (Anacardiaceae) and were called "ponticulus" (a small bridge) (Joel and Eisenstein 1980). In *P. vera*, once a pollen tube has passed through the ponticulus, in this region of the funicle, there is an accumulation of callose that prevents growth of later pollen tubes (Martinez-Pallé and Herrero 1995). Because in both *Pistacia* and *Amphipterygium* the dorsal part of the funicle contacts the stylar canal in a similar way, it is also likely that in *Amphipterygium*, pollen tubes reach the ovule via this pathway (ponticulus). In *Pistacia* species, pollen tubes reaching the embryo sac via the chalaza have been reported (Copeland 1955; Grundwag and Fahn 1969; Grundwag 1976; Martinez-Pallé and Herrero 1995; Shuraki and Sedgley 1997). Interestingly, other studies report chalazogamy for some other rosids that are wind pollinated and have a delay between anthesis and maturity of the embryo sac (Sogo and Tobe 2006). In *Juglans* (Juglandaceae), it was experimentally shown that chalazogamy is caused by immaturity of the ovule at the time the pollen tubes reach the ovary (Luza and Polito 1991).

Male Flowers

In both genera, the male flowers have a simple perianth of sepals (bracts?) and lack petals. The sepals are relatively thin and are not robust (narrow in *Amphipterygium*), and there is only one vascular trace. There is somewhat stronger evidence than in female flowers that these organs are sepals (and not bracts) because in *Amphipterygium*, they are basally united, and in *P. lentiscus*, each organ has a common base with the stamen of the same radius. However, a comparative study with other Anacardiaceae is necessary to resolve the question of homology. Sepal and stamen number is variable (four to seven) in both genera but in many species commonly five. The gynoecium is highly reduced (present as a tiny rudiment in *P. lentiscus* and completely absent in *Amphipterygium*). The stamens tend to alternate with the sepals in both genera. However, in some *Pistacia* species, they tend to be in the same radii or to be lacking. The stamens have large elongate anthers but short filaments. The anthers are introrse (almost latrorse in *Amphipterygium*), although they are slightly ventrifixed (almost basifixed in *Amphipterygium*). Stomata are lacking in stamens (Endress and Stumpf 1991). The anthers have hairs, mainly in the apical region, i.e., the peripheral area of the floral bud, in *Amphipterygium* and *Pistacia malayana* (Ding Hou 1978; Endress and Stumpf 1991).

Pollen grains are highly similar in the two genera (see also Erdtman 1952). They are spherical and have more than three (up to 12) small, roundish apertures that are somewhat protruding and are irregularly sculptured. The extra-apertural

exine is microreticulate, and the muri have a verrucate ornamentation.

Relationship of Amphipterygium *and* Pistacia *and Position in Anacardiaceae*

The inclusion of the ex-Julianiaceae in Anacardiaceae and relationships to *Pistacia* have been proposed several times (Stern 1952; Young 1976; Petersen and Fairbrothers 1983; Wannan and Quinn 1990; Aguilar-Ortigoza et al. 2003; Aguilar-Ortigoza and Sosa 2004; Pell 2004). Wannan (2006), in a structural cladistic study, even found *Orthopterygium* sister to a clade formed by *Amphipterygium* and *Pistacia*. Although many of their shared features are not exclusive to these genera, when compared with other Anacardiaceae, some of them bear striking similarities and especially concern the development of the gynoecium and ovule (Bachelier and Endress 2005). The combination of a unitegmic ovule with an extremely enlarged funicle with a set of a median and several lateral appendages is a unique shared feature of the two genera. Although conspicuous funicles are characteristic for the entire family Anacardiaceae (Kelkar 1958; Robbertse et al. 1986; von Teichman 1988*a*, 1988*b*, 1991*a*, 1991*b*, 1992, 1993, 1994, 1998; von Teichman and van Wyk 1996; Carmello-Guerreiro and Sartori Paoli 1999, 2005), their relative size and complexity in *Amphipterygium* and *Pistacia* are outstanding. *Amphipterygium* is further evolved than *Pistacia* in the reduction and complete loss of the opposite sex in the unisexual inflorescences, the loss of the perianth in female flowers, and the formation of cupules, which completely and permanently enclose a single fertile fruit.

Another member of Anacardiaceae with cupulelike structures surrounding groups of fruits is *Blepharocarya*. However, the cupule in this genus is very different from that in *Amphipterygium* in detail, and the female flowers are less similar to those of both *Amphipterygium* and *Pistacia*. Although the three genera share a unilocular gynoecium with a single ovule, *Blepharocarya* has a style ending in a single, small stigma with a single PTTT and a bitegmic ovule with a ventral, semiapical placenta; in addition, it has a nectary disk (Wannan et al. 1987; J. B. Bachelier, personal observations).

With the former Anacardieae (*sensu* Engler 1892) (*Anacardium* and *Mangifera*), *Amphipterygium* and *Pistacia* share a unilocular ovary and a unitegmic ovule with a basal placenta (Copeland 1961; Joel and Eisenstein 1980; Moncur and Wait 1986; de Wet et al. 1986). However, they have a (potentially monomerous; Copeland 1961) gynoecium with a long style, a small stigma, and a single PTTT, a constantly pentamerous perianth with sepals and petals and a nectary (not disk-shaped).

With the former Semecarpeae (*sensu* Engler 1892), *Amphipterygium* and *Pistacia* share a unilocular ovary with a style ending in three (bilobed) stigmas (pseudomonomerous gynoecium), but the flowers of Semecarpeae commonly have a pentamerous double perianth with calyx, corolla, and a nectary disk, and the bitegmic ovule has a ventral apical insertion (Wannan and Quinn 1991).

The gynoecium structure of *Amphipterygium* and *Pistacia* is most similar to (other) members of the former Rhoeae (*sensu* Engler 1892). This is expressed in the degree of reduction of two of the three carpels in the pseudomonomerous ovary. Also, the gynoecium development of *Amphipterygium* (this study) and *Pistacia* (Payer 1857; Marchand 1869; Copeland 1955; Takeda et al. 1979; Martinez-Pallé and Herrero 1995; Hormaza and Polito 1996; Shuraki and Sedgley 1997; this study) considerably resembles that of *Rhus* (Baillon 1874; McNair 1921; Copeland and Doyel 1940; Sattler 1973; Gallant et al. 1998). *Lithraea*, another member of the former Rhoeae, shows interesting similarities with *Amphipterygium* and *Pistacia* in ovule structure (unitegmic, with a median outgrowth, similar to the tail in *Amphipterygum* and *Pistacia*) and basal-ventral placenta (Carmello-Guerreiro and Sartori Paoli [2005] imprecisely say "basal-lateral").

In the basalmost Anacardiaceae (Spondioideae) and the sister family Burseraceae, the ovules are bitegmic. The micropyle is formed predominantly by the inner integument, whereas the outer is shorter (*Buchanania* and Burseraceae). In Spondioideae and Anacardioideae, the outer integument is somewhat detached from the inner one, is flappy, and does not take part in the micropyle features that also tend to be common in other malvids (Endress and Matthews 2006). The unitegmic condition is thus derived in Anacardiaceae because it has been reported in only a few Anacardioideae, including *Amphipterygium*, *Pistacia*, and *Lithraea*. Wannan's (2006) report of unitegmy in a genus of Spondioideae (*Tapirira*) is probably based on a misinterpretation of the original source (von Teichman 1990).

Within Anacardiaceae, *Amphipterygium* and *Pistacia* share many floral similarities with the former Anacardieae and Rhoeae *sensu* Engler (1892). These two tribes do not represent clades (Terrazas 1994; Pell 2004), but almost all of their components are in Anacardioideae, the largest subfamily of Anacardiaceae, together with *Amphipterygium* and/or *Orthopterygium* and *Pistacia* (Wannan and Quinn 1990, 1991; Terrazas 1994; Aguilar-Ortigoza and Sosa 2004; Pell 2004; Wannan 2006).

Conclusion

This is the first detailed account of the branching pattern of the female inflorescence and the structure of the samaroid unit of *Amphipterygium* and the first detailed morphological study of the floral structure of ex-Julianiaceae compared with a closely related genus in Anacardiaceae. There are striking similarities in the gynoecium development and the structure of the unitegmic ovule with an exceedingly massive and complex funicle with particular appendages in the two genera.

This strongly supports the recognition of the ex-Julianiaceae as a member of the Anacardiaceae, although the actual lack of resolution of the intergeneric and intrageneric relationships within the family makes the interpretation of the ovule appendages in terms of homology or homoplasy difficult. More studies on the development of pseudomonomerous tricarpellate gynoecia in other genera of the former Rhoeae and an improvement of the phylogeny of the family (S. Pell, personal communication) are necessary.

Pistacia seems to be a good candidate for evo-devo investigations on the reduction of one of the two sexes in unisexual flowers and on the unusual differentiation of the ovule-funicle complex. Whether the funicle appendages are linked to a modification of the meristem of the reduced outer integument remains a question to tackle.

Acknowledgments

We thank David H. Lorence, Ralph Manzanell, and Dominique Bachelier for collecting valuable material. The late William Klein is thanked for allowing P. K. Endress to collect material in the National Tropical Botanical Garden, Kauai, Hawaii. We are grateful to Rosemarie Siegrist for support with microtome sectioning and Urs Jauch for support with SEM. We also thank an anonymous reviewer for valuable comments on the manuscript.

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Annals of Botany **102**: 539–550, 2008
doi:10.1093/aob/mcn139, available online at www.aob.oxfordjournals.org

OXFORD JOURNALS
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Floral Structure of *Kirkia* (Kirkiaceae) and its Position in Sapindales

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Received: 6 May 2008 Returned for revision: 11 June 2008 Accepted: 26 June 2008 Published electronically: 7 August 2008

• *Background and Aims* The monogeneric Kirkiaceae (Sapindales) were formerly placed as Kirkioideae in Simaroubaceae. However, recent molecular phylogenetic studies indicate that they are not in Simaroubaceae and they appear to be sister to the clade of Anacardiaceae plus Burseraceae. Such affinity was never considered or discussed since the first description of *Kirkia*. The present study is the first detailed analysis of the floral structure of a representative of Kirkiaceae and the first comparison with other sapindalean families, especially Anacardiaceae and Burseraceae.
• *Methods* Floral structure of *Kirkia wilmsii* was studied using transversal and longitudinal microtome section series, scanning electron microscopy and light microscopy.
• *Key Results* The flowers of *Kirkia wilmsii* are morphologically bisexual but functionally unisexual. They are polysymmetric, isomerous (tetramerous) and haplostemonous. The ovary is syncarpous and entirely synascidiate. The floral apex forms a hemispherical protrusion on top of the ovary. The styles are free but postgenitally united and apically form a stigmatic head with a compitum. Each carpel is uniovulate (biovulate in a few other species) and ovules are crassinucellar, bitegmic and slightly campylotropous. The micropyle is formed by both integuments and is unusually long. The unusual two radially disposed locules in each carpel in the former genus *Pleiokirkia* can be explained developmentally by the two offset and tightly contiguous lateral placentae.
• *Conclusions* Paralleling the molecular results, a suite of floral features supports the position of Kirkiaceae close to the Anacardiaceae–Burseraceae clade, and not in Simaroubaceae.

Key words: Kirkiaceae, floral structure, gynoecium, Sapindales, Anacardiaceae, Burseraceae, monoecy, functional dioecy, heterodichogamy.

INTRODUCTION

Kirkia Oliver is a sapindalean genus with six species of small to medium-sized trees in eastern tropical Africa, South Africa and Madagascar (Engler, 1897; Stannard, 1981, 2007). Oliver (1868*a*, *b*) first described *Kirkia* and included it in Simaroubaceae (as *Simarubeae*). Engler (1896) also placed it in Simaroubaceae and established the monotypic tribe Kirkieae in Simarouboideae, one of the four subfamilies he circumscribed. Three new species were later added to the genus when Engler (1931*c*) raised Kirkieae to subfamilial level. Based on a similar fruit structure but double the number of carpels, Capuron (1961) described a monotypic genus *Pleiokirkia*, endemic to Madagascar, and considered it to be close to *Kirkia*. The close relationship between *Kirkia* and *Pleiokirkia* was also supported by fruit anatomy (Fernando and Quinn, 1992). *Pleiokirkia* was later sunk into *Kirkia* (Stannard, 2007).

The affinities of *Kirkia* within Simaroubaceae remained uncertain for a long time despite comparative studies on wood anatomy (Webber, 1936; Heimsch, 1942; Metcalfe and Chalk, 1950), pollen morphology (Erdtman, 1952), gynoecium structure (Ramp, 1988), fruit structure (Fernando and Quinn, 1992) and phytochemistry (Polonsky, 1983; da Silva and Gottlieb, 1987; Simão *et al.*, 1991; Mulholland *et al.*, 2003). Potential relationships of *Kirkia* with other sapindalean families were never suggested, although Oliver (1868*b*, p. 27) mentioned that it could be a Burseraceae.

Molecular phylogenetic studies showed that Simaroubaceae are an artificial taxon made up partly of only distantly related components currently placed in Sapindales and Malpighiales (Irvingiaceae), or unplaced in malvids (Picramniaceae) (Fernando *et al.*, 1995; Stevens, 2001 onwards). That *Kirkia* forms a family, Kirkiaceae, was first suggested by Takhtajan (1966). But its position within Sapindales remained uncertain (Bakker *et al.*, 1998; Fernando *et al.*, 1995; Gadek *et al.*, 1996; Muellner *et al.*, 2007). Depending on taxon sampling, and DNA regions and methods used, Kirkiaceae either appear toward the base of the Sapindales (Gadek *et al.*, 1996; Bakker *et al.*, 1998) or as sister to the Anacardiaceae–Burseraceae clade (Fig. 1; Gadek *et al.*, 1996; Fernando *et al.*, 1995; Muellner *et al.*, 2007).

Apart from a short account on the gynoecium (Ramp, 1988), the present analysis of the floral structure is the first in a representative of the family Kirkiaceae. Furthermore, a comparison with the floral structure of the clade Anacardiaceae plus Burseraceae is made possible by the comparative studies on floral morphology plus anatomy and development, with special emphasis of the gynoecium in both families (Bachelier and Endress, 2007; J. B. Bachelier and P. K. Endress, unpubl. res.), and also by the studies on aspects of floral structure in Anacardiaceae by Wannan and Quinn (1991) and Wannan (2006).

MATERIALS AND METHODS

Flowering material of *Kirkia wilmsii* Engl. fixed in FAA was provided by Mrs D. Fourie (no collection number), National

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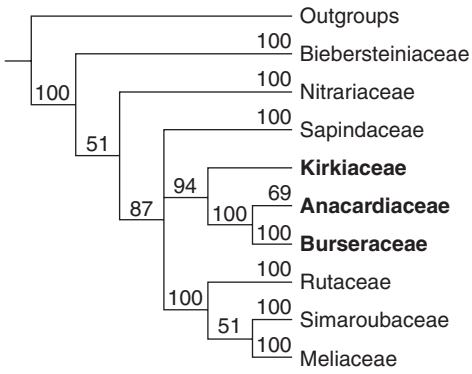

FIG. 1. Phylogenetic relationships in Sapindales, based on *rbc*L sequences (Bayesian posterior probabilities indicated above the branches; simplified from Muellner *et al.*, 2007).

Botanical Garden, Pretoria (South Africa), to E. Ramp in 1987. The material was studied using light microscopy (LM) and scanning electron microscopy (SEM). For LM investigations, the material was embedded in Kulzer's Technovit 7100 (2-hydroxyethyl methacrylate), following a protocol adapted from Igersheim (1993) and Igersheim and Cichocki (1996). Serial microtome sections were made at 5, 7 or 10 μm, using a Microm HM 355 rotary microtome and a standard microtome knife D. The sections were stained with ruthenium red and toluidine blue, and mounted in Histomount (protocol adapted from Weber and Igersheim, 1994). For SEM investigations, specimens were stained with 2 % osmium tetroxide, dehydrated in ethanol and acetone, critical-point dried and sputter coated with gold, and studied at 20 kV with a Hitachi S-4000 scanning electron microscope. The fixed material and permanent slides of serial microtome sections are deposited at the Institute of Systematic Botany, University of Zürich (Z).

RESULTS

Morphology

The flowers are arranged in compound thyrsoids with the cymes dichasial and in higher branching orders monochasial. Although functionally unisexual, the flowers are always morphologically bisexual. They are polysymmetric and isomerous, and mostly tetramerous (Figs 2 and 3). Pentamerous or hexamerous flowers are also found on some low branching orders, and trimerous flowers on high branching orders.

The flowers are relatively small (<1 cm in diameter). They have long, jointed pedicels and a broad floral base. They are haplostemonous, with the stamens alternipetalous and the carpels antepetalous (Figs 3 and 4A). A short floral cup is formed by congenitally united petal and stamen bases (Fig. 3C, G, H).

Sepals are free and triangular (Fig. 2A–C). They are contiguous (valvate) in early stages of development but later the floral base and floral cup enlarge and thus their aestivation becomes open (Fig. 2A–D). The base of the sepals takes part in the floral cup but their extended margins remain free and overlap basally (Figs 2D and 3C, G, H). In tetramerous flowers, the sepals are arranged in pairs with the outer pair in median position (Figs 2A–C and 3). In pentamerous flowers, their aestivation is quincuncial at the base.

Petals are free, linear and acute (Fig. 2A, F). Basally, they expand between the sepal margins with a dorsal bulge (Fig. 4A). In contrast to the sepals, their aestivation is basally open but it is imbricate further up (Fig. 2A, E) and two patterns are observed in tetramerous flowers: (1) one petal inside, one petal outside, and two in between (Fig. 3A, B), or (2) two petals outside and two inside (Fig. 3E, F). The petals protect the inner floral organs in

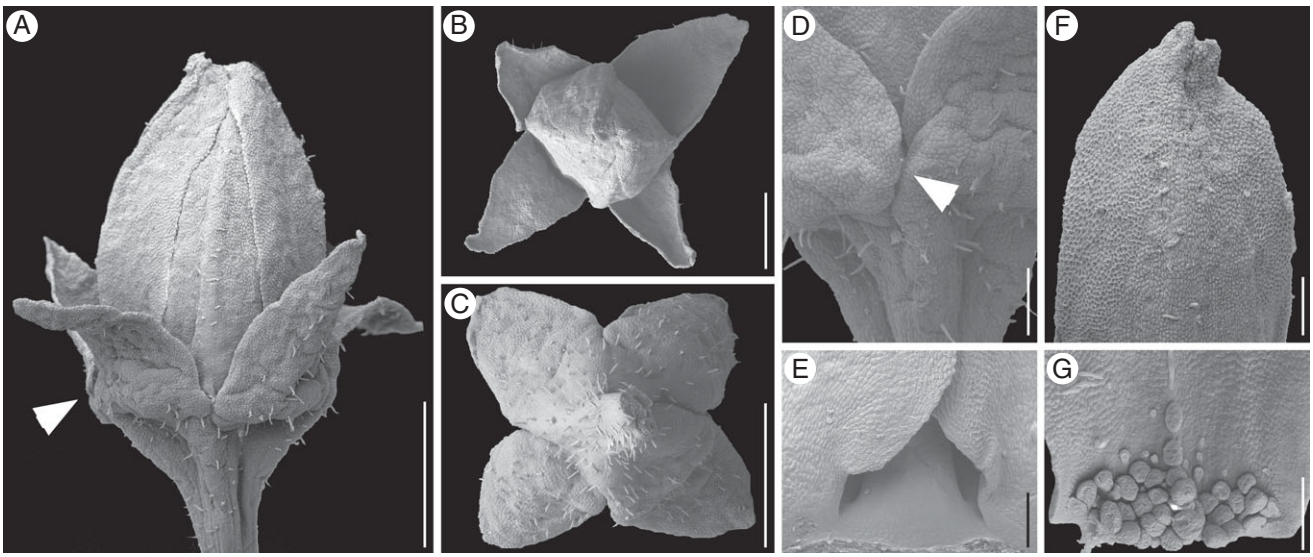

FIG. 2. *Kirkia wilmsii*. Flower buds and parts of flower buds. (A) Bud, lateral view, arrowhead points to close-up in (D). (B) Same bud, from above, with sepals arranged in decussate pairs. (C) Another bud, from below, with sepals arranged in decussate pairs. (D) Bud shown in (A), lateral view, close-up on floral base and overlapping sepal margins (arrowhead). (E) Petal aestivation basally open and imbricate further up. (F) Petal tip, dorsal side. (G) Carpet of secretory hairs on inner side of petal base. Scale bars: A, C = 400 μm; B = 200 μm; D, E, F, G = 100 μm.

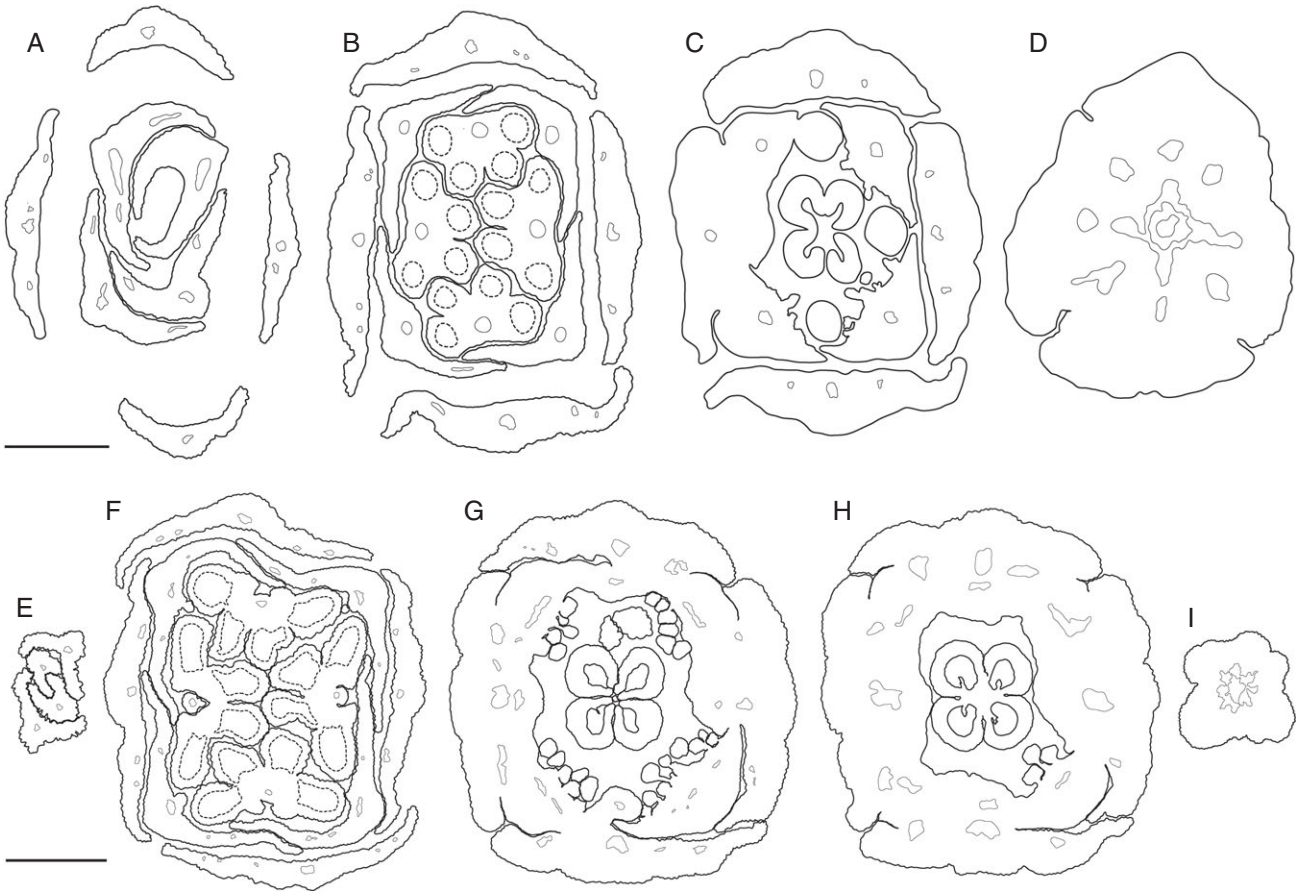

FIG. 3. *Kirkia wilmsii*. Transverse microtome section series of two flower buds. Morphological surfaces drawn with thick continuous lines; secondary morphological surfaces drawn with thick dashed lines; vascular bundles drawn with thin continuous lines. (A–D) Male flower bud: (A) open sepal aestivation and imbricate petal tips; (B) contiguous (valvate) sepal aestivation and imbricate petal bases, showing two pairs of antesepalous stamens and introrse anthers with a broad and thick connective; (C) valvate sepal bases and floral cup formed by fusion of the central part of sepal bases, and petal and stamen bases, showing secretory hairs on the inner side of the petal bases and four antepetalous (delayed) sterile carpels; (D) floral base. (E–I) Sterile flower bud: (E) imbricate petal tips, arranged in pairs; (F) sepals and petals arranged in pairs, two pairs of antesepalous sterile stamens, with anthers dorsifixed basally and filament attachment hidden in a pseudopit (for term see Endress and Stumpf, 1991); (G) overlapping free sepal margins and floral cup formed by fusion of the central part of sepal bases, and petal and stamen bases, showing the carpet of secretory hairs on the inner side of the petal bases and four antepetalous carpels; (H) dorsal side of petal bases expanding between the free sepal bases and floral cup surrounding a (sterile) syncarpous and synascidiate ovary with four aborted ovules; (I) pedicel. Scale bars: A–D = 200 μm; E–I = 500 μm.

late bud when they become longer than the sepals or even earlier when sepal aestivation changes from valvate to open. Postgenital coherence between the overlapping margins of the petals is formed by interdentation of their papillate surface and striate cuticular ornamentation. At anthesis, the expanded petals are curved slightly inwards and their basal dorsal bulges push the sepal margins away from each other. The arrangement of the sepals in decussate pairs is more conspicuous because the outer pair appears inserted below the inner pair. Calyx and corolla are widely open and androecium and gynoecium are thus exposed (Fig. 4A; see also figures in Immelman, 1984).

Stamens have a broad and thick filament base that narrows and becomes more round further up, and a sagittate and slightly apiculate anther (Fig. 4A). Anthers are dorsally basifixed (Fig. 4A–G). The transition from filament to anther is hidden by the dorsal parts of the thecae, which curve backwards around the constricted tip of the filament and form a pseudopit (Fig. 4D, G; a pit open on one side, here the dorsal side; for term see Endress and Stumpf, 1991). The connective is thick and broad (Fig. 3B, F). Each anther has a shallow dorsal and a deep ventral median (longitudinal) furrow (Fig. 3B, F). The anther is broader on the dorsal than the ventral side, and is thus introrse (Figs 3B, F and 4B, D, E, G). The dehiscence lines extend from the tip of the thecae down to their base and encompass their lower shoulders (Fig. 4B, C, E, F). In our material, the flowers of the low branching orders of the inflorescence had sterile anthers and were thus functionally female (Fig. 4A). In contrast, in flowers terminating axes of higher branching orders, the anthers were more developed than the carpels, and thus were more likely functionally male (Fig. 3A–D). In some flowers, both sexes appeared abortive (Fig. 3E–I). A thick and lobed intrastaminal nectary disc is present but expands only late in development (Figs 4A and 5A).

The gynoecium is of angiospermy type 4 (Fig. 5; carpels closed entirely by postgenital fusion; for term see Endress

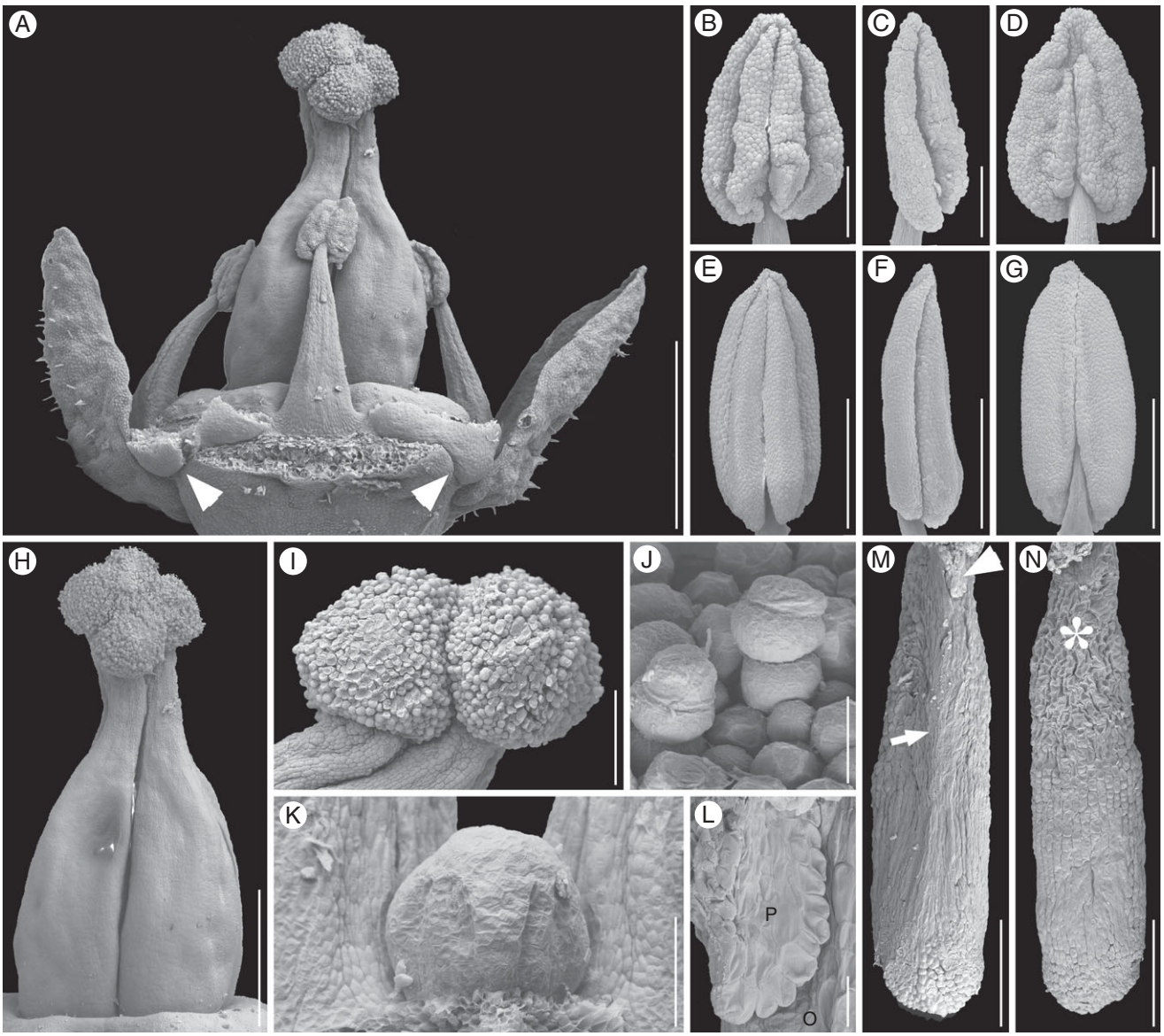

FIG. 4. *Kirkia wilmsii*. Reproductive structures. (A) Preanthetic female flower, lateral view, perianth partly removed; arrowheads pointing to protruding petal bases. (B–G) Anthers: (B–D) sterile anther of anthetic female flower; (E–G) fertile anther of male flower bud; (B, E) ventral view; (C, F) lateral view; (D, G) dorsal view, filament attachment hidden between thecae. (H) Preanthetic gynoecium of the flower in (A), lateral view. (I) Same gynoecium, close-up of stigmatic head, lateral view. (J) Stigmatic papillae. (K) Hemispherical protrusion above the ovary, lateral view. (L) Sterile placenta (P) (with collapsed epidermal cells) appressed to the base of the (fertile) ovule (O). (M, N) Fertile ovule: (M) raphal side with arrowhead pointing to sterile placenta and arrow pointing to raphe; (N) antiraphal side with asterisk indicating collapsed enlarged cells of outer integument. Scale bars: A = 500 μm; B, C, D, I, M, N = 90 μm; E, F, G, H = 200 μm; J, L = 10 μm; K = 50 μm.

and Igersheim, 2000). Superficially, the entire gynoecium gives the impression of being apocarpous because the dorsal part of the carpels is conspicuously bulging (Fig. 4A, H). However, the gynoecium has a syncarpous superior ovary with a short stalk (gynophore) (Fig. 5A, I–N). Above the ovary, the gynoecium is apocarpous (Fig. 5A–H). However, the free parts of the carpels are contiguous, form a conical stylar part (Fig. 5A, E–H), and are distally postgenitally united for half of their length (Fig. 5A–D). They form an oblique and flattened four-lobed receptive plate ('stigmatic head'), each lobe corresponding to the tip of a carpel (Figs 4A, H, I and 5A, B). The free part of the carpels is plicate and has a ventral median longitudinal slit extending from the stigma down to the ovary (Fig. 5A–H). The (united) stigmas form an external compitum (Fig. 5A, B). The stigmatic surface has unicellular (spherical) and uniseriate multicellular (moniliform) papillae (Figs 4J and 6A) and is covered with secretion. Four pollen tube transmitting tracts differentiate downwards in the inner angle of the ventral slit of the carpels (Fig. 5A–H). Below the short compitum, they extend separately toward the base of the stylar canals and the placentae (Fig. 5A, C–I). The gynoecium is entirely synascidiate in the ovary (Fig. 5A, I–M). A symplicate

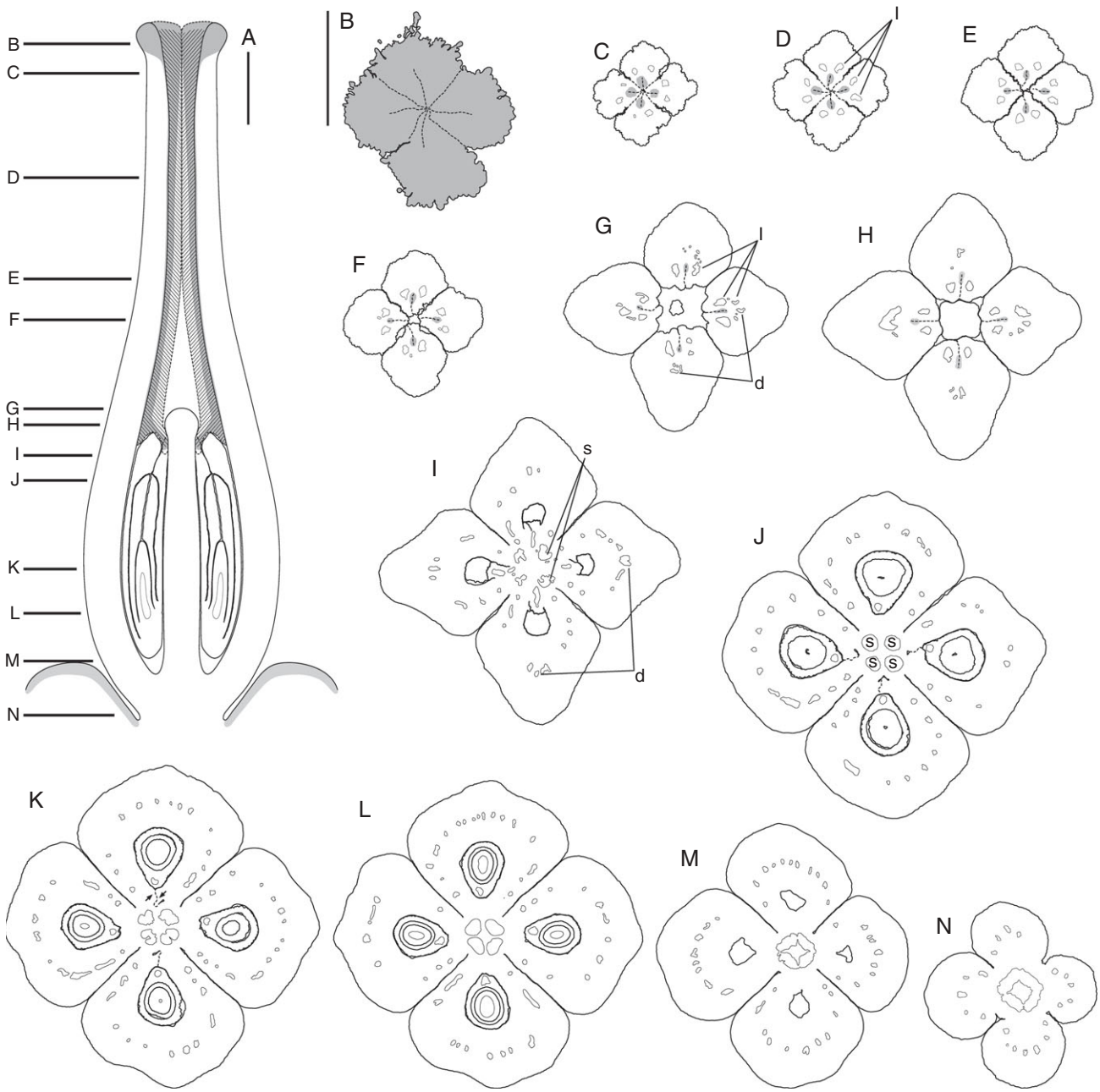

FIG. 5. *Kirkia wilmsii*. Anthetic gynoecium. Morphological surfaces drawn with thick continuous lines; thick dashed lines used in (A) for parts outside the median plane of symmetry, in (B–N) for postgenitally united surfaces; vascular bundles drawn with thin continuous lines; pollen tube transmitting tract dark grey. d, Dorsal vascular bundle; l, lateral vascular bundle; s, synlateral vascular bundle. (A) Schematic median longitudinal section of gynoecium and nectary disc (light grey); postgenitally united surfaces hatched. (B–N) Transverse microtome section series; (B) stigmatic head; (C, D) postgenitally united distal parts of the carpels; (E, F) connivent but free parts of the carpels; (G, H) connivent bases of the free parts of the carpels around the hemispherical protrusion on top of the ovary; (I–M) synascidiate ovary, the two arrows in (K) pointing to the S-shaped line formed by the two lateral placentae (compare with Figs 6F and 7A); (N) gynophore. Scale bars: A, B–N = 500 μm.

zone is lacking. Above the ovary, basally between the free parts of the carpels, there is a conspicuous hemispherical protrusion (Figs 4K, 5A, G, H and 6B).

The carpels are uniovulate (Fig. 5I–L). However, they have two axile and almost collateral placentae in the uppermost part of the locule (Figs 5I–K, 6F, G and 7A). The second placenta slightly protrudes in such a way that it resembles a second ovule aborting early in development (Fig. 4L, M). Behind the second placenta, toward the centre of the gynoecium, there is a small gap (Figs 6F–I and 7A). This may correspond to the 'inner locule' described in other *Kirkia* species (Fig. 7B; see Discussion; see also figures in Capuron, 1961).

The ovule is long and cylindrical (Fig. 4M, N). It is crassinucellar, bitegmic, antitropous (ovule curvature direction opposite to direction of carpel involution; for term see

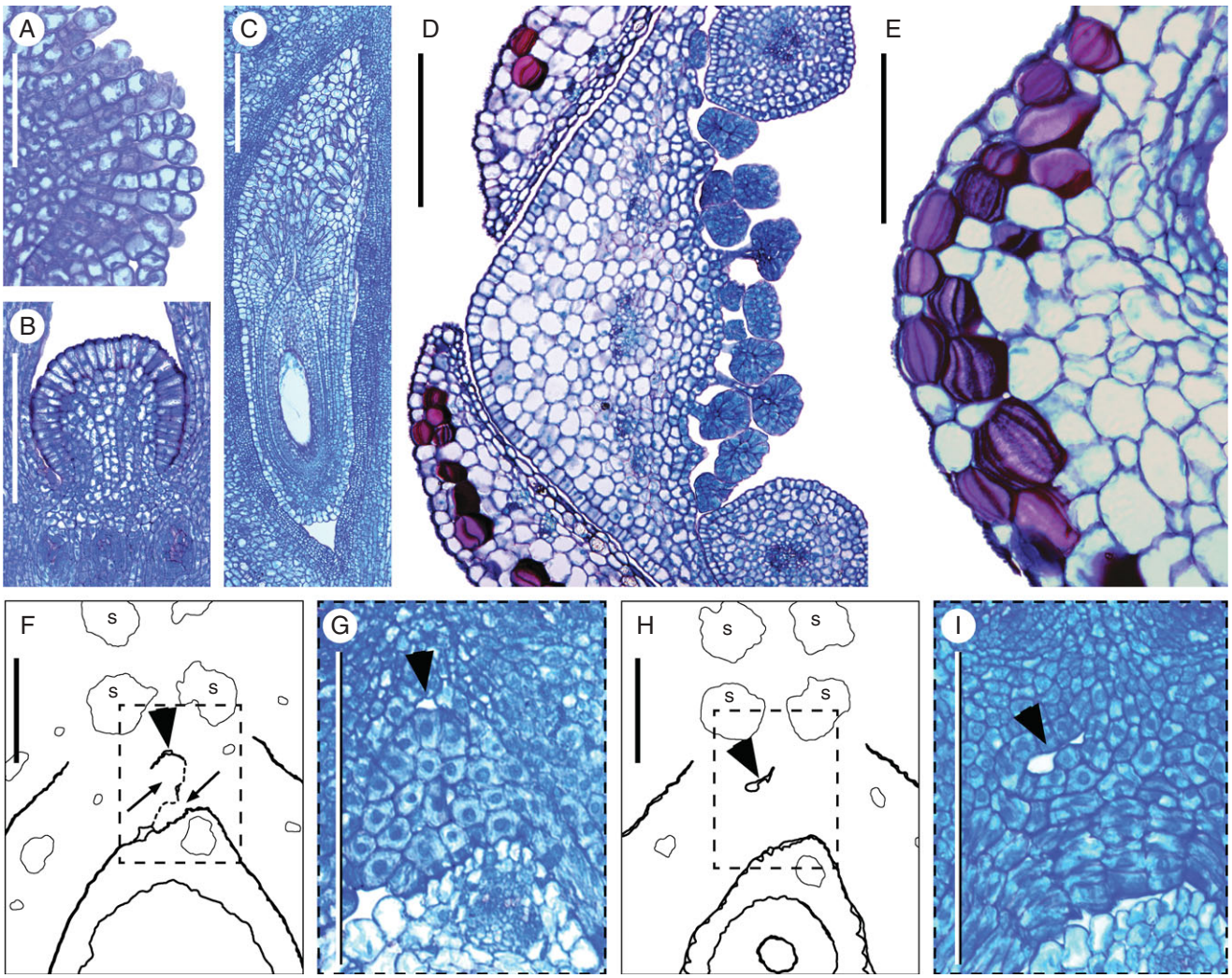

FIG. 6. *Kirkia wilmsii*. (A) Longitudinal section (LS) of uniseriate multicellular papillae of the stigma before anthesis. (B) LS of the hemispherical protrusion in the floral centre above the ovary (compare with Fig. 5A). (C) LS of the slightly campylotropous ovule filling the locule at anthesis, with the expanded large-celled distal parts of the two integuments forming a long micropyle. (D) Transverse section (TS) of base of sepals, petal and stamens before anthesis, showing carpet of secretory hairs (with short multiseriate stalk and large multicellular head) on the inner side of the petal base, and petal base expanding dorsally between the free margins of two sepal bases. (E) LS of sepal base showing the epidermal and sub-epidermal special mucilage cells. (F–I) TS of a preanthetic gynoecium and corresponding enlarged micrographs, showing the inner angle of a fertile locule and centre of the gynoecium (locule dorsal side oriented downwards; compare with Fig. 5K); arrows point to placentae; arrowhead points to the second reduced locule developing on the same radius as the fertile one (compare with Fig. 7A); morphological surfaces drawn with thick continuous lines; postgenitally fused morphological surfaces drawn with dashed lines; vascular bundles drawn with thin continuous lines; 's': synlateral vascular bundle; dash rectangles in (F) and (H) show location of (G) and (I). (F, G) In the upper part of the locule, the endocarp differentiation begins laterally and the ventral inner surface of the carpel is S-shaped (arrowhead). (H, I) Lower down, the endocarp encompasses the inner angle of the locule and the second locule is isolated (arrowhead). Scale bars: A = 30 μm; B, C, D = 200 μm; E, F, G, H, I = 100 μm.

Endress, 1994), and slightly campylotropous with only the very base of the nucellus and embryo sac curved (Fig. 5A). The two integuments surround the nucellus and, although both appear to be of the same thickness, the inner integument comprises three or four cell layers but the outer only two or three cell layers (Figs 5A and 6C). Above the nucellus the integuments are elongate and thickened. At anthesis, the inner integument is about twice as long as the nucellus and the outer even two and a half times (Figs 5A and 6C). Thus, the micropyle is unusually long and comprises two distinct zones. The proximal zone is a straight tubular canal formed by the inner integument, whereas the distal zone is not tubular and is somewhat wavy, and is formed by the second integument (Figs 5A and 6C). The extended part of the integuments above the nucellus comes about by cell enlargement (Fig. 6C). In isolated ovules studied with the SEM, these enlarged cells tend to collapse (Fig. 4 N). The ovule fills the locule and the micropyle is contiguous with the placenta (Fig. 5A).

Anatomy

Sepals have one median and two lateral main vascular bundles, which extend almost through their whole length,

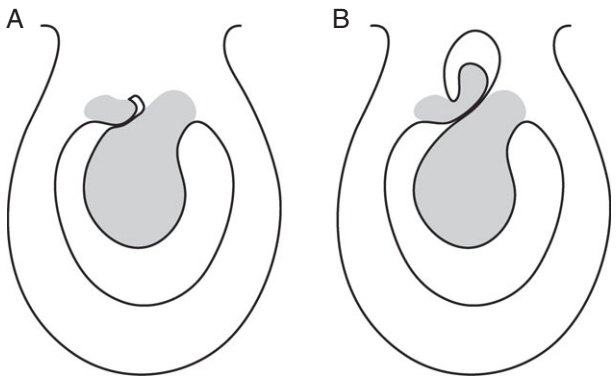

FIG. 7. Transverse section diagrams of a carpel: (A) *Kirkia wilmsii* with one locule and a small inner opening; (B) *Kirkia leandrii* ('*Pleiokirkia*') with two 'locules', the inner one corresponding to the small inner opening in *Kirkia wilmsii*.

and may have one to two smaller, additional lateral bundles in their free parts (Fig. 3A–C, F–H). Toward the sepal base, the smaller lateral bundles merge with one of the two main lateral bundles before extending into the floral base (Fig. 3G, H). Petals have one median main vascular bundle (Fig. 3A–C, E–H) and can have up to three pairs of smaller, lateral bundles at anthesis. Toward the petal bases, all lateral bundles merge together with the main median bundle and a single petal trace extends downwards (Fig. 3C, D, G, H). Stamens have a single bundle, which extends into the upper half of the anthers (Fig. 3B, C, F–H).

In carpels, a pair of lateral vascular bundles differentiates just below the stigmatic head on each side of the ventral slit (Fig. 5C). These laterals extend downwards into the ovary and form synlaterals in the synascidiate zone (Fig. 5D–J). At the upper end of the locule, each synlateral gives off a branch serving an adjacent ovule (Fig. 5I) and ending in the chalaza, whereas lower down, the synlaterals converge toward the centre of the gynoecium and form a ring-shaped central vascular complex (Fig. 5K–N).

In contrast, distinct dorsal bundles are present only far below the zone of postgenital union of the free upper carpel parts (Fig. 5G). Between the dorsal and lateral bundles there are numerous smaller bundles and together they form a reticulate system above the ovary and extend downwards around the locules (Fig. 5G–M). They merge in the gynophore with the ring of the synlaterals.

In the floral base, the petal traces merge with the lateral traces of the sepals whereas the stamen traces merge with the median sepal traces of the same radius. All vascular bundles converge toward the central vasculature of the gynoecium and form a stele with it (Fig. 3D, I).

Histology

Lignified unicellular hairs are sparsely present on the floral base and the dorsal side of sepals, the petal parts, which are not covered by another petal in bud, and the ventral side of the petal base (Figs 2A, C, D, F, G and 4A). Stomata are present on the dorsal side of sepals and petals, on the smooth surface of the nectary disc, and on the carpel tips below the stigmatic head. On the ventral side of the petal bases, there is a carpet of hairs with a multicellular multiseriate stalk and massive head containing dark-staining cells (Figs 2G, 3C, G, H and 6D). Epidermal and subepidermal special mucilage cells (Fig. 6D, E; cells with thickened mucilaginous, layered inner tangential wall; for term see Matthews and Endress, 2006) are present in the sepals and floral base in late buds and anthetic flowers.

DISCUSSION

Sexual system

The presence of functionally unisexual (but morphologically bisexual) flowers appears to be common in Kirkiaceae (this study; Oliver, 1868*a*; Capuron, 1961; Stannard, 1981; Immelmann, 1984), and is also common in Anacardiaceae, Burseraceae and other Sapindales (J. B. Bachelier and P. K. Endress, unpubl. res.). Functional dioecy by flushes of male and female flowers as described by Immelmann (1984) for *Kirkia wilmsii* may be morphologically reflected by the presence of female flowers in the lower order branches of the cymes of the thyrsoid inflorescences, and male flowers in the higher order branches, and sequential opening of flowers of successive branching orders (this study). This is a kind of dichogamy and even (imprecise) heterodichogamy if the flowering schemes of different individuals by Immelman (1984) are considered. Heterodichogamy is uncommon in angiosperms (Renner, 2001) but was also recorded among Sapindales, in several species of *Acer* and in *Cupania* (Sapindaceae) (Gabriel, 1968; de Jong, 1976; Bawa, 1977; Tatsuhiro, 2000; Sato, 2002; Gleiser and Verdú, 2005; Renner *et al.*, 2007; Kikuchi and Shibata, 2008). The same pattern in the distribution of male and female flowers within an inflorescence as in *Kirkia* has also been reported in *Anacardium* (Anacardiaceae) (Copeland, 1962; Moncur and Wait, 1986; Moncur, 1988), in *Cedrela*, *Melia* and *Toona* (Meliaceae) (Styles, 1972; Gouvêa *et al.*, 2008*a*, *b*), and in *Cupania* (Sapindaceae) (Bawa, 1977). In another type of heterodichogamy (in *Hernandia*, Laurales) it was also found that male and female flowers had a specific distribution pattern in the inflorescence (Endress and Lorence, 2004). Based on inflorescence structure it is to be expected that hitherto unrecognized cases of heterodichogamy may occur among Sapindales.

Floral merism

Flowers in most species of Kirkiaceae are tetramerous and isomerous (Stannard, 1981). Of special interest is the occurrence of species with double the number of carpels, still in one whorl (Capuron, 1961; Stannard, 1981). The tendency of an increase in carpel number is also present in Anacardiaceae (*Pleiogynium*, up to 13; Wannan and Quinn, 1991) and Burseraceae (*Beiselia*, up to 12; Forman *et al.*, 1991), and in other families of Sapindales, such as Meliaceae (*Turraea*, up to 20; Harms, 1940), Rutaceae (*Aegle*, up to 20; Vasil and Johri, 1964), and also in the

unplaced possibly sapindalean fossil *Landeenia*, approx. 18 (Manchester and Hermsen, 2000). This tendency occurs even more generally in the entire malvids (Endress and Matthews, 2006). Another pattern of interest is the co-occurrence of tetramerous and pentamerous flowers on the same individual, with the pentamerous ones especially on lower-order axes of the inflorescence, as also known from some Rutaceae (*Ruta*, Eichler, 1878; *Skimmia*, personal observation). In *Kirkia wilmsii* trimerous, tetramerous, pentamerous and hexamerous, isomerous, flowers were found on the same individual. Floral isomery is also common in Rutaceae (Engler, 1931*b*; Gut, 1966; Ramp, 1988) and Simaroubaceae (Engler, 1931*c*; Ramp, 1988) but less so in Anacardiaceae and Burseraceae (Engler, 1931*a*; J. B. Bachelier and P. K. Endress, unpubl. res.). Rutaceae also exhibit many genera with tetramerous flowers. In contrast, in Anacardiaceae pentamerous flowers are common, and in Burseraceae trimerous flowers (Lam, 1932; J. B. Bachelier and P. K. Endress, unpubl. res.). However, all numbers, three, four and five, combined with isomery, are present in Anacardiaceae, Burseraceae and Kirkiaceae (and other Sapindales) in different frequencies and distribution. Whereas in Burseraceae isomerous flowers are common, as in Kirkiaceae, in Anacardiaceae they are largely restricted to Spondioideae (S. Pell, Brooklyn Botanical Garden, unpubl. res.).

Floral cup and perianth

The flowers have an expanded base and a shallow floral cup bearing the nectary disc. The cup is formed by the congenitally united bases of petals and stamens, and the median parts of the sepals. The sepal margins remain free and extend downwards as ledges for a short distance. Such free sepal margins on a floral cup or on a floral base without a cup are not restricted to Sapindales but also occur in other rosid groups. Although they are involved in the formation of the floral cup, sepals and petals are free among themselves, thus the perianth is chorisepalous and choripetalous in Kirkiaceae, as in many other Sapindales. According to Merxmüller and Heine (1960), in *Kirkia dewinteri*, the calyx is united for one-third of its length. If this is correct there would be free and united calyces in the genus.

Sepals are deltoid and have three main vascular traces and thus exhibit the shape and vasculature that is common in many rosids. The petals are acuminate and have a single vascular trace. They become longer than the sepals in older buds and thus have a protective function at this stage in Kirkiaceae, Anacardiaceae and Burseraceae, as also found in various other rosids (e.g. most Celastrales, some Oxalidales, some Crossosomatales and a few Chrysobalanaceae *sensu lato*; Matthews and Endress, 2002, 2005*a*, *b*, 2008). Sepal aestivation of young floral buds is commonly valvate in Kirkiaceae, as in Burseraceae and some Anacardiaceae. However, it becomes open in older buds when the petal bases expand between the sepal bases, as also observed in *Bursera* (Burseraceae) (J. B. Bachelier and P. K. Endress, unpubl. res.). Petal aestivation is mainly imbricate and sometimes valvate (Oliver, 1868*a*, *b*; Stannard, 1981) in Kirkiaceae. Dense groups of secretory hairs with a short multiseriate stalk and large multicellular head at the inner base of the petals in *Kirkia* (see also Stannard, 1981) are unusual because they were not found in other areas of the flowers. In *Beiselia* there are secretory hairs with a large multicellular head, especially on the adaxial surface of the petal tips, but they have a uniseriate multicellular stalk as do all secretory hairs in Anacardiaceae and Burseraceae studied (J. B. Bachelier and P. K. Endress, unpubl. res.). These secretory hairs with multiseriate stalk may thus be an apomorphy for Kirkiaceae. Their concentration and restriction to a small area of the flower is suggestive of a specific function. However, since a disc that looks like a normal nectary is present, it is unlikely that the hairs are nectariferous (as is the case in the perianth of some Malvaceae; Vogel, 2000) (see below). It would be of interest to study the hairs in live material.

Androecium

Haplostemony, the presence of only one stamen whorl as consistent in Kirkiaceae is unusual for Burseraceae and occurs in only few genera (*Triomma*, some species of *Canarium*, *Santiria*, *Protium* and *Crepidospermum*; Leenhouts, 1956; Daly, 1989; Mitchell and Daly, 1993). In Anacardiaceae, haplostemonous flowers only occur in some Anacardioideae (Mitchell and Daly, 1993). The stamens of haplostemonous flowers are alternipetalous in all three families. Flowers with two stamen whorls in Anacardiaceae and Burseraceae (J. B. Bachelier and P. K. Endress, unpubl. res.) and other Sapindales (Rutaceae, Beille, 1902; Eckert, 1966; Gut, 1966; Simaroubaceae, Nair and Joseph, 1957; Nair and Joshi, 1958; Narayana and Sayeeduddin, 1958; Eckert, 1966) are commonly obdiplostemonous, i.e. the antepetalous stamens have a smaller base than the antesepalous ones, and, in isomerous flowers, the carpels are positioned in the antepetalous radii (contrary to expectation based on regular alternation of whorls) because there is more space available in this position. That the anthetic antepetalous stamens are less developed is commonly obvious also by their shorter filaments, as in Anacardiaceae and Burseraceae (J. B. Bachelier and P. K. Endress, unpubl. res.), and is a common situation also in many other rosids. Haplostemonous flowers with alternipetalous stamens as in Kirkiaceae may be seen as an extreme case in this trend: as complete suppression of the antepetalous stamens. Among other Sapindales, flowers in Meliaceae are mostly obdiplostemonous, rarely diplostemonous (with the carpels alternipetalous), sometimes haplostemonous with the carpels antepetalous, rarely alternipetalous (Harms, 1940); in haplostemonous Rutaceae the stamens are alternipetalous (Beille, 1902; Engler, 1931*b*), in Simaroubaceae alternipetalous (*Brucea*, *Picrasma*) or antepetalous (*Picrolemma*, Engler, 1931*c*). Thus the position of stamens in haplostemonous flowers in families of Sapindales other than the clade of Kirkiaceae–Anacardiaceae–Burseraceae appears less fixed.

Stamen shape in Kirkiaceae corresponds to a common type in Sapindales and other rosids with sagittate, slightly dorsifixed, introrse anthers, and with a relatively narrow transition region between filament and anther (Endress and Stumpf, 1991; Matthews and Endress, 2002, 2004,

2005*a*, *b*, 2006, 2008; Bachelier and Endress, 2007; J. B. Bachelier and P. K. Endress, unpubl. res.). Especially interesting in *Kirkia* is the presence of a pseudopit, the enclosure of this transition region between the two dorsal pollen sacs. Among rosids this feature is especially common in Sapindales and was reported for some Anacardiaceae and Burseraceae (Endress and Stumpf, 1991; J. B. Bachelier and P. K. Endress, unpubl. res.).

Nectary disc

A conspicuous intrastaminal nectary disc with nectar pores, often separating the androecium base from the gynoecium base for some distance, as in *Kirkia*, is also present in Burseraceae and most Anacardiaceae, as well as in Meliaceae, Rutaceae and Simaroubaceae. In Sapindaceae (and *Mangifera* of Anacardiaceae), the nectary disc is, however, extrastaminal (Ronse De Craene and Haston, 2006).

Gynoecium

The unusual ovary structure in *Kirkia* can be better understood when fruit differentiation is considered. The dispersal unit is a mericarp which develops from the outward bulging dorsal region of the carpels (including the locule) and detaches from a central part that remains as a column, called the 'central column' (Capuron, 1961) or 'carpophore' (Engler, 1931*c*; Stannard, 1981). This carpophore originates by histological differentiation from the central part of the synascidiate ovary. Such mericarps are not present in Anacardiaceae and Burseraceae. In Simaroubaceae carpels are dispersed individually, which was probably one reason why *Kirkia* was formerly included in Simaroubaceae. However, the morphological basis is different, since in Simaroubaceae the gynoecium is more or less entirely apocarpous (with the styles only postgenitally united) (Nair and Joseph, 1957; Nair and Joshi, 1958; Narayana and Sayeeduddin, 1958; Endress *et al.*, 1983; Ramp, 1988). More or less apocarpous gynoecia (with the styles only postgenitally united) are also present in part of Rutaceae (Gut, 1966; Endress *et al.*, 1983; Ramp, 1988).

Another unusual trait in the ovary is the reported presence of two locules per carpel in radial disposition, each with an ovule, in the former genus *Pleiokirkia* (Capuron, 1961). This may also be the case in other species of *Kirkia* (Stannard, 1981). Whereas a compartmentalization of each carpel into two collateral locules is known in various groups of angiosperms, a radial disposition of two locules is highly unusual and morphologically puzzling. However, the analysis of the gynoecium structure in *K. wilmsii* in the present publication allows a morphological explanation of the two radially disposed locules in the former genus *Pleiokirkia*. Although in *Pleiokirkia* there are two ovules, the ovule of the inner locule aborts, and although in *Kirkia* there is only one ovule, there are two placentae. These placentae are not collateral but somewhat radially displaced.

As in the former *Pleiokirkia*, only the outer placenta bears a fertile ovule whereas the inner one bears no ovule at all. The two placentae are tightly pressed together as seen in transverse sections, so that the inner surface of the carpels is more or less S-shaped. The fertile locule is on the outer side of the S. As a counterpart, there is a minute gap on the inner side of the S (Figs 6F and G and 7A) which may correspond to the inner locule in the former *Pleiokirkia* (Fig. 7B). Such transition between the presence of one and two ovules is also present in the Anacardiaceae–Burseraceae clade, with two more or less collateral ovules in most Burseraceae, and one ovule in most Anacardiaceae. Interestingly, there are also rare cases of the reverse situation in the two families: two ovules (the second epitropous) in *Dracontomelon* (J. B. Bachelier and P. K. Endress, unpubl. res.) and in *Spondias* (Baillon, 1874), one ovule in *Beiselia* (J. B. Bachelier and P. K. Endress, unpubl. res.) and in *Boswellia* (Sunnichan *et al.*, 2005). However, if two ovules are present, the placentae are collateral and not or less radially displaced.

The stigmatic head, a conspicuous feature in *Kirkia*, consists of the postgenitally united free carpel tips. This construction allows the formation of a compitum, which is absent lower down in the gynoecium because of the apocarpous stylar part and the completely synascidiate ovary. Such an organization of a stigmatic head is also known from Burseraceae but less so from Anacardiaceae (J. B. Bachelier and P. K. Endress, unpubl. res.). A stigmatic head is also present in the more or less completely apocarpous gynoecia of Rutaceae–Rutoideae and Simaroubaceae (Endress *et al.*, 1983), and also occurs in Meliaceae (Gouvêa *et al.*, 2008*a*, *b*), in which the gynoecium is usually described as syncarpous ('carpels united', Cronquist, 1981; Takhtajan, 1997). However, there are no critical studies on the internal morphological carpel surfaces in Meliaceae, and thus it is uncertain whether the style is really syncarpous or consists only of postgenitally united carpels, although there are some publications with line drawings of transverse sections of styles, which suggest true syncarpy (Narayana, 1958*a*, *b*, 1959*a*; Nair, 1962; Murty and Gupta, 1978*a*, *b*; Lal, 1994). The styles are truly syncarpous in Rutaceae–Citroideae (Ramp, 1988). In both Meliaceae and Rutaceae–Citroideae at least the stigmatic head appears to be apocarpous but the carpels are postgenitally united (Ramp, 1988; Gouvêa *et al.*, 2008*a*, *b*). The stigma in *Kirkia* is wet and exhibits unicellular and uniseriate pluricellular (moniliform) papillae, which are also present in Anacardiaceae and Burseraceae (Bachelier and Endress, 2007; J. B. Bachelier and P. K. Endress, unpubl. res.). This differs from the survey in Heslop-Harrison and Shivanna (1977) who reported a non-papillate (smooth) stigma for the only studied genus (*Cotinus*) of the Anacardiaceae–Burseraceae clade.

A further unifying trait in the gynoecium of Sapindales is the presence of an extensive remnant of the floral apex in the centre of the gynoecium that is not incorporated into the gynoecium architecture. In *Kirkia*, it forms a dome-shaped or almost spherical protrusion between the carpels where they are free above the synascidiate zone. In groups with entirely apocarpous (only postgenitally united) carpels (e.g. some Rutaceae, Simaroubaceae; Nair and Joshi, 1958; Ramp, 1988), it is present at the base between the free carpels. As the apically postgenitally united carpels are connivent, the protrusion cannot be seen from the outside.

This protrusion is commonly hidden in taxa with postgenitally united stigmas/styles (e.g. *Beiselia*, Burseraceae; *Dracontomelon*, Anacardiaceae; Rutaceae, Simaroubaceae; J. B. Bachelier and P. K. Endress, unpubl. res.). It is, however, exposed in gynoecia without intercarpellary postgenital union (e.g. *Pleiogynum*, *Spondias p.p.*, *Poupartiopsis*, Spondioideae; Mitchell *et al.*, 2006; J. B. Bachelier and P. K. Endress, unpubl. res.). On architectural grounds the dome is especially large in gynoecia with an increased number of carpels (Endress, 2006). Interestingly, a symplicate zone is lacking in Kirkiaceae and in Spondioideae (Anacardiaceae), or very short in *Beiselia* (Burseraceae). In contrast, in core Burseraceae, a symplicate zone is present and extends from the synascidiate base of the gynoecium to the base of the stigmatic head (J. B. Bachelier and P. K. Endress, unpubl. res.).

Ovules

The crassinucellar, bitegmic ovules in *Kirkia* are antitropous (epitropous) as are those of Burseraceae (and also Rutaceae, Simaroubaceae and Meliaceae), while those of Anacardiaceae (and also Sapindaceae) are syntropous (apotropous). They are slightly campylotropous (especially involving the basal area of the nucellus), a trait also shared with other Sapindales, especially Burseraceae (Wiger, 1935; Narayana, 1959*b*, 1960*a*, *b*; J. B. Bachelier and P. K. Endress, unpubl. res.), Simaroubaceae (Wiger, 1935; Narayana, 1957), Rutaceae (Mauritzon, 1935; Boesewinkel, 1977, 1984; Souza *et al.*, 2003), and Sapindaceae (e.g. Weckerle and Rutishauser, 2003, 2005). In contrast, Anacardiaceae tend to have anatropous ovules (Bachelier and Endress, 2007; J. B. Bachelier and P. K. Endress, unpubl. res.). The inner integument is thicker than the outer in *Kirkia*, another tendency shared by many Sapindales and other malvids (Endress and Matthews, 2006).

A peculiarity of the ovules of *Kirkia* is that they have an exceedingly long micropyle formed by elongation of both integuments. Conspicuous is the cell enlargement of the outer integument accompanying the elongation. These features were not observed in Anacardiaceae and Burseraceae and have not been reported from other Sapindales, and may thus be autapomorphies for *Kirkia*. The micropylar part of the outer integument is conspicuously wavy. Such wavy micropyles (but in the inner integument, with the outer not involved in micropyle formation) were illustrated for some other Sapindales as well (Burseraceae; Narayana, 1959*b*, J. B. Bachelier and P. K. Endress, unpubl. res.; Simaroubaceae; Narayana, 1957; Nair and Sukumaran, 1960).

Systematic aspects

Do features of floral structure support the removal of Kirkia from Simaroubaceae and a close relationship with the Anacardiaceae–Burseraceae clade, as is suggested by molecular phylogenetic studies (Muellner *et al.*, 2007)? As seen from the comparative morphological studies on Kirkiaceae (this study) and Anacardiaceae and Burseraceae (J. B. Bachelier and P. K. Endress, unpubl. res.) and from comparison with published work on Sapindales, there is indeed a suite of features that appears to be synapomorphic for Kirkiaceae and Anacardiaceae plus Burseraceae. The pronounced convex remnant of the floral apex on top of the syncarpous and entirely synascidiate ovary, and the almost complete absence of a symplicate zone in the gynoecium, as in *Beiselia* (Burseraceae) and Spondioideae (Anacardiaceae), appear to be unique for this clade, as they are not known from any other family of Sapindales (not recorded in Simaroubaceae: Engler, 1931*c*; Nair and Joseph, 1957; Nair and Joshi, 1958; Narayana and Sayeeduddin, 1958; Ramp, 1988; Meliaceae: Garudamma, 1957; Narayana, 1958*a*; Nair, 1962, 1963; Murty and Gupta, 1978*a*, *b*; Lal, 1994; Rutaceae: Gut, 1966; Ramp, 1988; Sapindaceae: Weckerle and Rutishauser, 2003, 2005; Nitrariaceae: Nair and Nathawat, 1958; Ronse De Craene *et al.*, 1996; Biebersteiniaceae: floral structure unstudied). This suite of characters is often associated with an increased number of carpels in a whorl (e.g. more than five in otherwise pentamerous flowers). However, it is also present in *Kirkia* with only four carpels and some Spondioideae with only three to five carpels. Thus the unique architecture of the gynoecium is not necessarily dependent on an increase in carpel number.

A number of other features of Kirkiaceae occur widely in Sapindales and are thus probably plesiomorphic for the clade of Kirkiaceae and Anacardiaceae plus Burseraceae: anthers with pseudopit, campylotropous ovules, antitropous curvature of ovules, inner integument thicker than outer (Endress and Stumpf, 1991; Endress and Matthews, 2006), and the tendency to form gynoecia with an increased number of carpels (lacking in Simaroubaceae but also present in Rutaceae and Meliaceae). These features are probably synapomorphic at the level of Sapindales or even malvids (see Endress and Matthews, 2006).

CONCLUSIONS

The present comparative study of floral structure is the first in the family Kirkiaceae. It also provides the first structural comparison of Kirkiaceae with the Anacardiaceae–Burseraceae clade within Sapindales. Both the sister relationship of Kirkiaceae and the Anacardiaceae–Burseraceae clade and a more distant relationship with Simaroubaceae, as found in molecular phylogenetic studies, are supported by floral structural features. The unusual two radially disposed locules per carpel in the former genus *Pleiokirkia* can be explained developmentally by the two offset lateral placentae. The results are a step to a better understanding of the floral evolution in Sapindales.

ACKNOWLEDGEMENTS

We thank Eduard Ramp for kindly providing fixed material of *Kirkia wilmsii* and microtome sections, which were used in addition to our own section series. We acknowledge the Brunei Forestry Department and Brunei Herbarium for support in the collection of material of Anacardiaceae and Burseraceae. We also thank Joffre Haji Ali Ahmad for organizing the collection trips and Jangarun Eri for his expertise in the field. The Georges-und-Antoine-Claraz-Schenkung is

thanked for financial support of the field trip. We thank Mary Endress for reading the manuscript, and two anonymous reviewers for their detailed comments on the manuscript.

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Botanical Journal of the Linnean Society, 2009, **159**, 499–571. With 49 figures

Comparative floral morphology and anatomy of Anacardiaceae and Burseraceae (Sapindales), with a special focus on gynoecium structure and evolution

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Received 12 December 2008; accepted for publication 20 February 2009

Anacardiaceae and Burseraceae are traditionally distinguished by the number of ovules (1 vs. 2) per locule and the direction of ovule curvature (syntropous vs. antitropous). Recent molecular phylogenetic studies have shown that these families are sister groups in Sapindales after having been separated in different orders for a long time. We present a comparative morphological study of the flower structure in both families. The major clades, usually supported in molecular phylogenetic analyses, are well supported by floral structure. In Anacardiaceae, there is a tendency to gynoecium reduction to a single fertile carpel (particularly in Anacardioideae). The single ovule has a long and unusually differentiated funicle, which connects with the stylar pollen tube transmitting tract in all representatives studied. In Anacardiaceae–Spondiadoideae, there is a tendency to form an extensive synascidiate zone, with a massive remnant of the floral apex in the centre; these features are also present in *Beiselia* (Burseraceae) and Kirkiaceae (sister to Anacardiaceae plus Burseraceae) and may represent a synapomorphy or apomorphic tendency for the three families. In core Burseraceae, gynoecium structure is much less diverse than in Anacardiaceae and has probably retained more plesiomorphies. Differences in proportions of parts of the ovules in Anacardiaceae and Burseraceae are linked with the different direction of ovule curvature. *Botanical Journal of the Linnean Society*, 2009, **159**, 499–571.

ADDITIONAL KEYWORDS: androecium – diplostemony – floral structure – malvids – obdiplostemony – perianth – ponticulus – resin canals – rosids – stigmatic head.

INTRODUCTION

Anacardiaceae and Burseraceae are mid-sized families of mainly tropical trees and shrubs, both with several hundred species in 60–75 and 18 genera, respectively (Clarkson, Chase & Harley, 2002; Weeks, 2003; Pell, 2004; Weeks, Daly & Simpson, 2005; Mitchell *et al.*, 2006). Anacardiaceae are well known from genera yielding economically important fruits (mangos, cashew nuts, pistachios); others are notorious for causing violent allergic skin reactions (poison ivy, see also Mitchell, 1990). Burseraceae are known for producing widely used incenses (frankincense, myrrh).

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Anacardiaceae and Burseraceae are currently placed in Sapindales (Fig. 1; Takhtajan, 1997; APG, 1998; Stevens, 2001 onwards; APG II, 2003; Thorne, 2007). They share many features and are traditionally distinguished by ovule number and the direction of ovule curvature (Engler, 1892, 1896, 1931d), a single syntropous (apotropous) ovule per locule in Anacardiaceae and two antitropous (epitropous) ovules per locule in Burseraceae (Fig. 2). Five tribes were recognized in Anacardiaceae and three in Burseraceae (Engler, 1892, 1912). Because Engler (1892, 1912, 1931d) gave much importance to the direction of ovule curvature, he placed the two families far apart from each other: Anacardiaceae in Sapindales and Burseraceae in Geraniales. However, the two families have such a similar vegetative morphology and anatomy that a closer relationship was strongly considered by other authors who placed both families

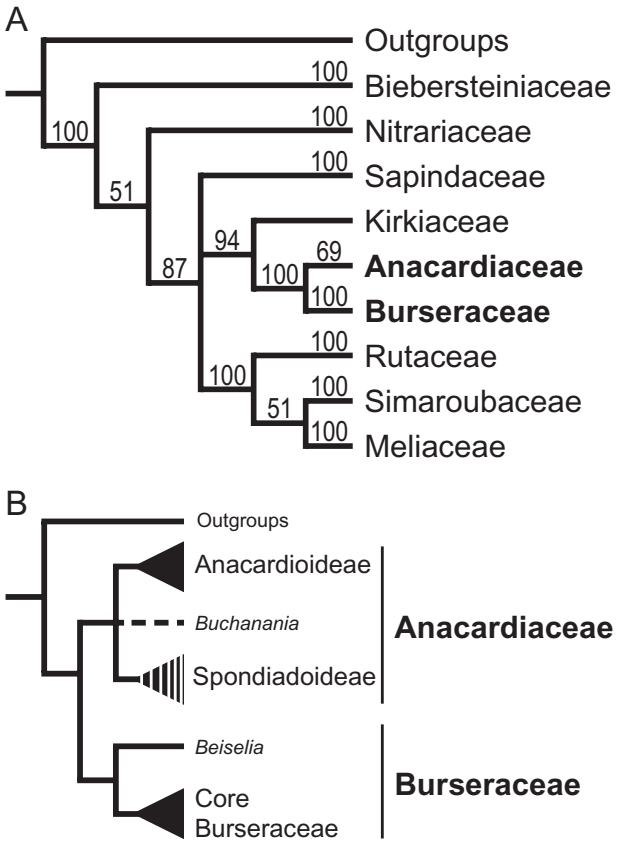


Figure 1. A, phylogeny of Sapindales, based on *rbc*L sequences (Bayesian posterior probabilities indicated above the branches; simplified from Muellner *et al.* (2007). B, phylogeny of major subclades of Anacardiaceae and Burseraceae, consensus based on several studies using molecular and non-molecular data (Terrazas, 1994; Clarkson *et al.*, 2002; Aguilar-Ortigoza & Sosa, 2004; Pell, 2004; Weeks *et al.*, 2005; Wannan, 2006).

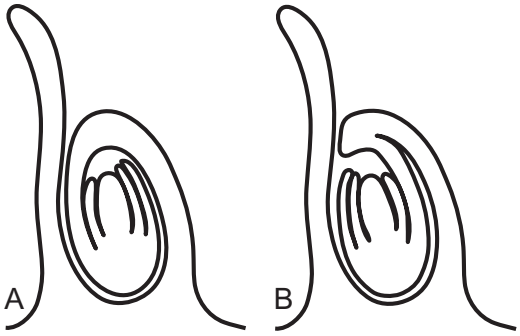


Figure 2. Direction of ovule curvature in the carpel. Schematic median longitudinal sections. A, syntropous (apotropous) ovule. B, antitropous (epitropous) ovule.

in the same order, Terebinthales ('Terebinthaceae', 'Térébinthinées' or 'Gruinales') (Baillon, 1874a; Eichler, 1878; Jadin, 1894; Hallier, 1908; Heimsch, 1942; also Engler in his earlier work, Engler, 1876). As various families (and genera) have both syntropous (apotropous) and antitropous (epitropous) ovules in a locule, it has even been suggested that the two families should be merged (Jadin, 1894). Depending on the significance given to the ovule structure, the relationships between Anacardiaceae and Burseraceae have long been debated. Thus, the single feature of ovule curvature direction played an important role in earlier discussions.

In phylogenetic studies based on molecular and/or non-molecular data, these two families together form a well-supported clade within Sapindales (Fig. 1A; Terrazas, 1994; Gadek *et al.*, 1996; Bakker *et al.*, 1998; Clarkson *et al.*, 2002; Pell, 2004; Weeks *et al.*, 2005; Wannan, 2006; Muellner, Vassiliades & Renner, 2007). Both families commonly appear to be monophyletic (Fig. 1B; Gadek *et al.*, 1996; Clarkson *et al.*, 2002; Pell, 2004; Weeks *et al.*, 2005). However, in some analyses, Burseraceae appear nested within Spondiadoideae Kunth ex Arn. of Anacardiaceae (Terrazas, 1994; Wannan, 2006).

In Anacardiaceae, four of the five tribes of Engler (1892) form a robust clade recognized as the large subfamily Anacardioideae Arn. (Fig. 1B) (Terrazas, 1994; Aguilar-Ortigoza & Sosa, 2004; Pell, 2004; Wannan, 2006). Within Anacardioideae, except for Dobineeae Pax (previously Podoaceae), which consistently appear to be sister to the remainder of the subfamily, phylogenetic resolution is poor (Pell, 2004). Anacardieae DC. (without *Buchanania* Spreng. and *Koordersiodendron* Engl.) form a clade with Semecarpeae Marchand and some genera of Rhoeae Voigt (e.g. *Faguetia* Marchand and *Schinus* L.) in most trees and they are all nested within the remainder of Rhoeae (excluding *Campnosperma* Thwaites and *Pentaspadon* Hook. f.) (Pell, 2004). In addition to Dobineeae, Anacardioideae also include the earlier recognized families Blepharocaryaceae (Bakker *et al.*, 1998; Aguilar-Ortigoza & Sosa, 2004; Wannan, 2006; Muellner *et al.*, 2007) and Julianiaceae (Pell, 2004; Wannan, 2006), which were both formerly erected as distinct families on the basis of their unusual inflorescences and infructescences, the structure of which was elucidated by Wannan, Waterhouse & Quinn (1987) and Bachelier & Endress (2007), respectively. The fifth tribe Spondiadeae Kunth ex DC. Engler (1892) forms the bulk of the much smaller subfamily Spondiadoideae (Terrazas, 1994; Aguilar-Ortigoza & Sosa, 2004; Pell, 2004; Wannan, 2006). However, the monophyly of Spondiadoideae is only weakly supported and sometimes they appear paraphyletic with respect to Anacardioideae (Pell, 2004; Wannan, 2006). In addition, Spondiadoideae comprise genera formerly placed in other tribes, such as *Buchanania* (Wannan,

2006; Pell & Mitchell, 2007) and, perhaps, *Androtium* Stapf (Engler, 1907), *Campnosperma*, *Koordersiodendron* and *Pentaspadon* (Wannan & Quinn, 1990, 1991; Wannan, 2006), which have not yet been included in any molecular phylogenetic studies. However, the position of the genus *Buchanania* remains uncertain (Fig. 1B). Depending on outgroups used and ingroup size, it appears nested within Spondiadoideae or as sister to the larger of the two subclades (Pell & Mitchell, 2007), to Anacardioideae (Bakker *et al.*, 1998; Aguilar-Ortigoza & Sosa, 2004; Muellner *et al.*, 2007; Pell & Mitchell, 2007) or to all other Anacardiaceae (Gadek *et al.*, 1996).

In Burseraceae, the three tribes circumscribed by Engler (1912) together form a well-supported clade (Clarkson *et al.*, 2002; Weeks *et al.*, 2005; Thulin *et al.*, 2008), which is here referred to as 'core Burseraceae' (Fig. 1). In this clade, two tribes, Canarieae Engl. and Protieae Marchand, appear to be monophyletic, whereas Bursereae DC. are paraphyletic (Clarkson *et al.*, 2002; Weeks *et al.*, 2005; Thulin *et al.*, 2008). Resolution within core Burseraceae is generally poor; Protieae tend to be sister to the subtribe Burserinae H. J. Lam, in which *Commiphora* Jacq. is either sister to or nested in *Bursera* Jacq. ex L. subgenus *Bursera* and Canarieae are nested in Boswelliinae H. J. Lam, with *Boswellia* Roxb. ex Colebr. and *Garuga* Roxb. sister to *Triomma* Hook. f. plus Canarieae (Clarkson *et al.*, 2002; Weeks *et al.*, 2005; Weeks & Simpson, 2007). However, in Thulin *et al.* (2008), Protieae are sister to the remaining core Burseraceae. The monotypic genus *Beiselia* Forman (Forman, 1987; Forman *et al.*, 1991) is consistently found as sister to core Burseraceae (Clarkson *et al.*, 2002; Weeks *et al.*, 2005; Thulin *et al.*, 2008).

Anacardiaceae and Burseraceae have similar wood anatomy, which is distinctive from other sapindalean families (Heimsch, 1942; Metcalfe & Chalk, 1950). Structural similarities are especially striking between Spondiadoideae and Burseraceae (Baillon, 1874a; Eichler, 1878; Jadin, 1894; Heimsch, 1942; Mitchell *et al.*, 2006; Wannan, 2006). A close relationship between Anacardiaceae and Burseraceae appears well supported by a large number of shared morphological and anatomical vegetative characters and, as stated by Kostermans (1991: 5), 'Anacardiaceae are certainly related to Burseraceae, all other assumptions should be referred to fantasy and should better be ignored'.

Nevertheless, no extensive comparative study of the floral structure has been carried out within or between the two families in the light of the new phylogenetic results. Earlier attempts probably failed because the flowers of Burseraceae and some Anacardiaceae are rich in tannins and it is almost impossible to make complete microtome section series with paraffin- or paraplast-embedded flowers. We therefore used plastic embedding medium. Our study is the first broad account of the comparative floral morphology and anatomy between the two families. It is also the first attempt to reconstruct the inner morphological surface of their gynoecium derived from the surface of the original floral apex (as outlined in Endress, 2006).

MATERIAL AND METHODS

Flowering material of the following taxa was studied:

Burseraceae

Beiselia mexicana Forman, female: A. Lau, s.n. (Mexico; Kew accession 49812.000); E. Ramp, 370 (cult., Städtische Sukkulentensammlung, Zürich, Switzerland); male: P. K. Endress, 6525; P. K. Endress, 6661; E. Ramp, 371 (cult., Städtische Sukkulentensammlung, Zürich, Switzerland);

Bursera sp.: U. Hofmann, s.n. (cult., Botanic Garden, University of Göttingen, Germany);

Canarium caudatum King: J. B. Bachelier, 42 (Brunei);

Commiphora caudata Engl., female: P. K. Endress, 03-82; male: P. K. Endress, 03-21 (both cult., National Tropical Botanical Garden, Kauai, Hawaii, USA);

Protium morii D.C.Daly: M.-F. Prévost & D. Sabatier, 4952 (cult., Botanic Garden of the IRD, Cayenne, French Guyana, France);

Protium obtusifolium March.: P.K. Endress, 03-74 (cult., National Tropical Botanical Garden, Kauai, Hawaii, USA);

Santiria cf. *apiculata* A. W. Bennett: J. B. Bachelier, 34 (Brunei).

Anacardiaceae

Anacardium occidentale L.: J. B. Bachelier, 3-04 (cult., Kourou, French Guyana, France); P. K. Endress, 3069 (cult., Kerala University, Trivandrum, India);

Blepharocarya involucrigera F. Muell., female: BPM. Hyland, 7614; male: P. K. Endress, 4229 (both Northern Queensland, Australia);

Buchanania arborescens (Blume) Blume: J. B. Bachelier, 33; J. B. Bachelier, 36; J. B. Bachelier, 37 (all Brunei); P. K. Endress, 9324 (cult., Botanic Garden Bogor, Java);

Campnosperma squamatum Ridley, female: J. B. Bachelier, 41; male: J. B. Bachelier, 39 (both Brunei);

Dracontomelon dao (Blanco) Merrill & Rolfe: J. B. Bachelier, 35 (cult., Arboretum of Brunei Herbarium, Brunei);

Mangifera indica L.: P. K. Endress, 1130 (cult., Escuela Agricola Panamericana, Zamorano, Honduras); P. K. Endress, 3071 (cult., Kerala University,

Trivandrum, India); P. K. Endress, 7338 (cult., Botanic Garden, University of Zürich, Switzerland);
Pleiogynium solandri (Benth.) Engl., female/male: P. K. Endress, 03-84/03-85 (cult., National Tropical Botanical Garden, Kauai, Hawaii, USA);
Pseudospondias longifolia Engl.: D. W. Thomas, 1059 (Cameroon; Kew accession 41220.000);
Pseudospondias microcarpa (A. Rich) Engl.: G. Troupin, 1059 (Democratic Republic of Congo; Kew accession 9845.000);
Schinus molle L.: J. B. Bachelier, s.n. (cult., Botanic Garden, University of Zürich, Switzerland);
Semecarpus australiensis Engl.: P. K. Endress, 9137 (cult., Arboretum, CSIRO, Atherton, Northern Queensland, Australia);
Semecarpus riparia Virot: J. Munzinger, 2540 (New Caledonia, France);
Solenocarpus philippinensis (Elmer) Kosterm.: T. Triono, 143 (Papua New Guinea; Kew accession 71258.000);
Spondias dulcis Forst.: J. B. Bachelier, 21 (cult., National Park of Temburong, Brunei);
Spondias purpurea L.: P. K. Endress, 1330 (cult., Cobán, Guatemala);
Tapirira sp.: J. B. Bachelier 2-04 (French Guyana, France).

Inflorescences, flowers and buds were fixed in formalin–acetic acid–alcohol (FAA) or 70% ethanol and studied using light microscopy (LM) and scanning electron microscopy (SEM). For LM investigations, the material was infiltrated and embedded in Kulzer's Technovit 7100 (2-hydroxyethyl methacrylate), following a protocol adapted from those of Igersheim (1993) and Igersheim & Cichocki (1996). The embedded material was sectioned at 5, 7 or 10 μm, depending on the parts and taxa, using a Microm HM 355 rotary microtome and a standard microtome knife D. The sections were stained with ruthenium red and toluidine blue (both from Fluka) following the protocol of Weber & Igersheim (1994), with specific adjustments according to the taxa, and mounted in Histomount. For SEM investigations, specimens were treated with 2% osmium tetroxide (Fluka), dehydrated in ethanol and acetone and critical-point dried. Specimens were mounted on stubs, sputter-coated with gold and studied at 20 kV with a Hitachi S-4000 scanning electron microscope. All vouchers and permanent slides of serial microtome sections are deposited at Institute of Systematic Botany, University of Zürich (Z).

General Comments on illustrations

Figures 3–39 represent structural analyses of each species studied. In schematic median longitudinal sections of gynoecia with an odd number of carpels two carpels are projected on the drawing plane. Morphological surfaces are drawn with thick continuous lines; pollen tube transmitting tracts are shaded dark grey (only in anthetic gynoecia); nectaries are shaded light grey. In transverse microtome section series, sections are ordered from the top downwards; postgenitally fused surfaces and pollen sacs are drawn with thick broken lines; vascular bundles are drawn with thin continuous lines and associated resin canals with thin broken lines. In median longitudinal sections, outlines of parts out of the median plane are drawn with thick broken lines; postgenitally fused surfaces are hatched; embryo sacs are drawn with thin continuous lines. Figures 40–48 are comparative plates of flowers, androecium, gynoecium and ovules, for each family. Figure 49 provides a summary for diversity of gynoecium morphology in Anacardiaceae, Burseraceae and Kirkiaceae.

Glossary

Angiospermy type 3: Carpel closed by complete postgenital fusion at the periphery but with an open canal in the inner angle of the ventral slit (Endress & Igersheim, 2000).

Angiospermy type 4: Carpel closed by complete postgenital fusion (Endress & Igersheim, 2000).

Anther with pseudopit: Anther with an almost closed furrow, in which the tip of the filament is inserted (and hidden) (Endress & Stumpf, 1991)

Antitropous: Ovule, in which the direction of curvature is opposite to the direction of carpel closure (Fig. 3B, see also Endress, 1994), more or less corresponding to epitropous (*sensu* Agardh, 1858).

Diplostemonous sensu lato: Flower with two whorls of stamens (irrespective of position of stamen whorls).

Diplostemonous sensu stricto: Flower with two whorls of stamens, in which the carpels are antesepalous (normal alternation of all floral organ whorls).

Obdiplostemonous: Flower with two whorls of stamens, in which the carpels are antepetalous and not antesepalous (here only used for isomerous flowers or flowers, in which the single fertile carpel is antepetalous). Traditionally used for flowers in which the outer whorl of stamens is antepetalous and the inner antesepalous. However, this usage is ambiguous because the antepetalous stamens may be much smaller than the antesepalous ones and then the

definition of 'inner' and 'outer' becomes blurred. Our definition is unambiguous.

Ponticulus (= small bridge): Zone of (postgenital) connection between ovule and pollen tube transmitting tract, located on the dorsal side of the funicle (see Joel & Eisenstein, 1980).

PTTT(s): Pollen tube transmitting tract(s).

Syntropous: Ovule, in which the direction of curvature is the same as the direction of carpel closure (Fig. 3A, see also Endress, 1994), more or less corresponding to apotropous (*sensu* Agardh, 1858).

RESULTS

Beiselia mexicana (Burseraceae) (Figs 3, 4, 40A–D, 43A, A′, 44A, 45A–C, 48A, B)

Morphology: The flowers are morphologically bisexual or male. They have a pentamerous perianth and androecium and two whorls of stamens (Figs 3, 40B–D). In morphologically bisexual flowers, the gynoecium comprises nine to 12 carpels (all fertile) (Figs 3C, 40D), whereas it is highly reduced in male flowers (Fig. 40A).

The sepals are congenitally united at the base. Their free parts are contiguous (valvate) in early stages but later their aestivation becomes open (Figs 3A–D, 40A). They differ in size, suggesting that the sepals are initiated in a spiral sequence (Fig. 3C, D). Petal aestivation is valvate with the united petal tips bent inwards (Fig. 3A–C) and shortly open basally (Fig. 3D). The corolla becomes longer than the calyx in young bud and protects the reproductive organs up to anthesis. Postgenital cohesion between the petal margins is formed by interdentation of their papillate surface and striate cuticular ornamentation. At anthesis, the united sepal bases bulge outwards and form a collar around the pedicel (Figs 3E, 40C). The expanded flat petals are acuminate, except for their tips, which retain the inward bend they had in bud (Figs 3A, 40A–D). The reproductive organs are entirely exposed (Fig. 40B, D).

The antepetalous stamens are slightly shorter and smaller than the antesepalous ones at all stages of development (Figs 3B, C, 40B). All stamens have a thick round filament base, which narrows towards the constricted tip, and a sagittate anther (Fig. 43A). The anthers are dorsifixed in their lower half and have a thin and narrow connective and a deep dorsal and a ventral longitudinal furrow. Their dorsal side is broader than the ventral side and the anthers are thus introrse (Fig. 44A). The dehiscence lines extend from the tip of the thecae down to their base and encompass their lower shoulders (Fig. 43A′). In our material, the stamens of morphologically bisexual flowers are sterile and the flowers are thus functionally female (Fig. 3). A lobed intrastaminal nectary disc is present. In female flowers it surrounds the ovary base (Fig. 40D) and in male flowers it covers a small conical bump in the centre, probably the remnant of the reduced gynoecium (Fig. 40A) ('ovariodisk', see Discussion on nectary).

The syncarpous gynoecium is polysymmetric (Figs 3B, C, 4B–M). However, the variable number of carpels often leads to a mismatch of the gynoecium symmetry planes with those of the perianth plus staminodes. The female flowers are thus not always strictly polysymmetric, in contrast to the male flowers (Fig. 40B). The gynoecium is conical, lacks a distinct style and ends in a large flat receptive plate (stigmatic head) (Fig. 45A–C). Between the carpels, longitudinal furrows extend from the stigma down to the ovary base (Fig. 45A, B). The gynoecium is of angiospermy type 3 (Fig. 4). The ovary and the major part above are synascidiate (Fig. 4A, H–M). It is followed by a short symplicate intermediate zone (Fig. 4A, F, G) and a distal apocarpous zone, in which, however, the carpels are not free but postgenitally united for most of their length (Fig. 4A–E). Each stigma is distally slightly reflexed and bilobed and has a shallow median ventral furrow (Fig. 4A–C). At anthesis, the papillate epidermis of the stigmas and their irregular multicellular protrusions are covered with secretion (Fig. 45B, C). The PTTTs converge toward the centre of the stigmatic head and form a compitum, which extends shortly downwards into the apocarpous but postgenitally united zone below the stigma (Fig. 4A–E). Lower down, each PTTT becomes more restricted to the inner angle of the ventral slit of each carpel. Above the synascidiate zone, the carpel flanks are no longer fused in the inner angle of the ventral slit and form a hollow canal down to the locule (Fig. 4A, H–J). It is unclear whether it is filled with secretion. In the synascidiate zone, each PTTT extends down to the placentae (Fig. 4A, H–K).

Each carpel has two superposed ovules per locule (Figs 4A, 48A, B). Because the numerous carpels are all in a whorl, the gynoecium has a large undifferentiated centre (Fig. 4A, I–L). Although the two ovules are superposed, the placentae are almost collateral. Ovules are crassinucellar, bitegmic and antitropous, with a short funicle inserted apically in the inner angle of the locule (Figs 4A, K, L, 48A). Both integuments are three cell layers thick, but the inner integument appears thicker than the outer one on the convex side (Fig. 4A).The outer integument is hood-shaped and forms short irregular lobes around the longer and papillate inner integument (Fig. 48A, B).

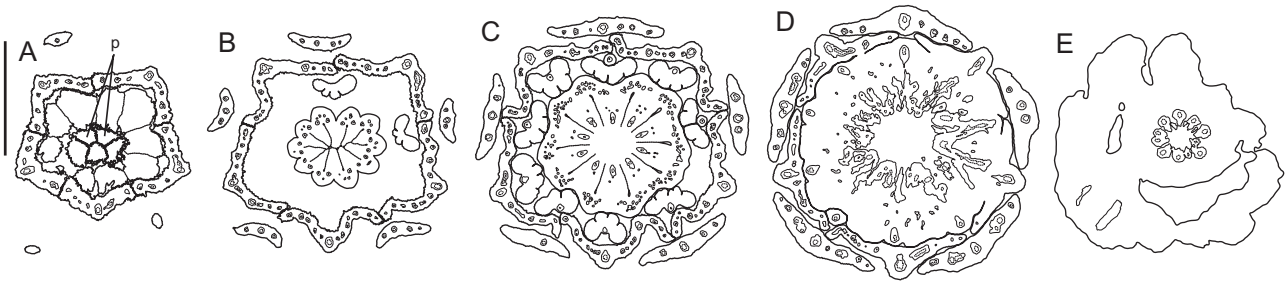


Figure 3. *Beiselia mexicana* (Burseraceae). Female flower bud, transverse section series. A, distal zone, petals valvate with tips (p) bent inwards in centre and surrounded by postgenitally united stigmas. B, sepals, petals valvate, anthers (sterile), gynoecium symplicate zone. C, anthers (sterile, one missing), gynoecium synascidiate zone. D, floral base, petal aestivation slightly open. E, sepal bases bulged backwards and surrounding the pedicel. Scale bar, 1 mm.

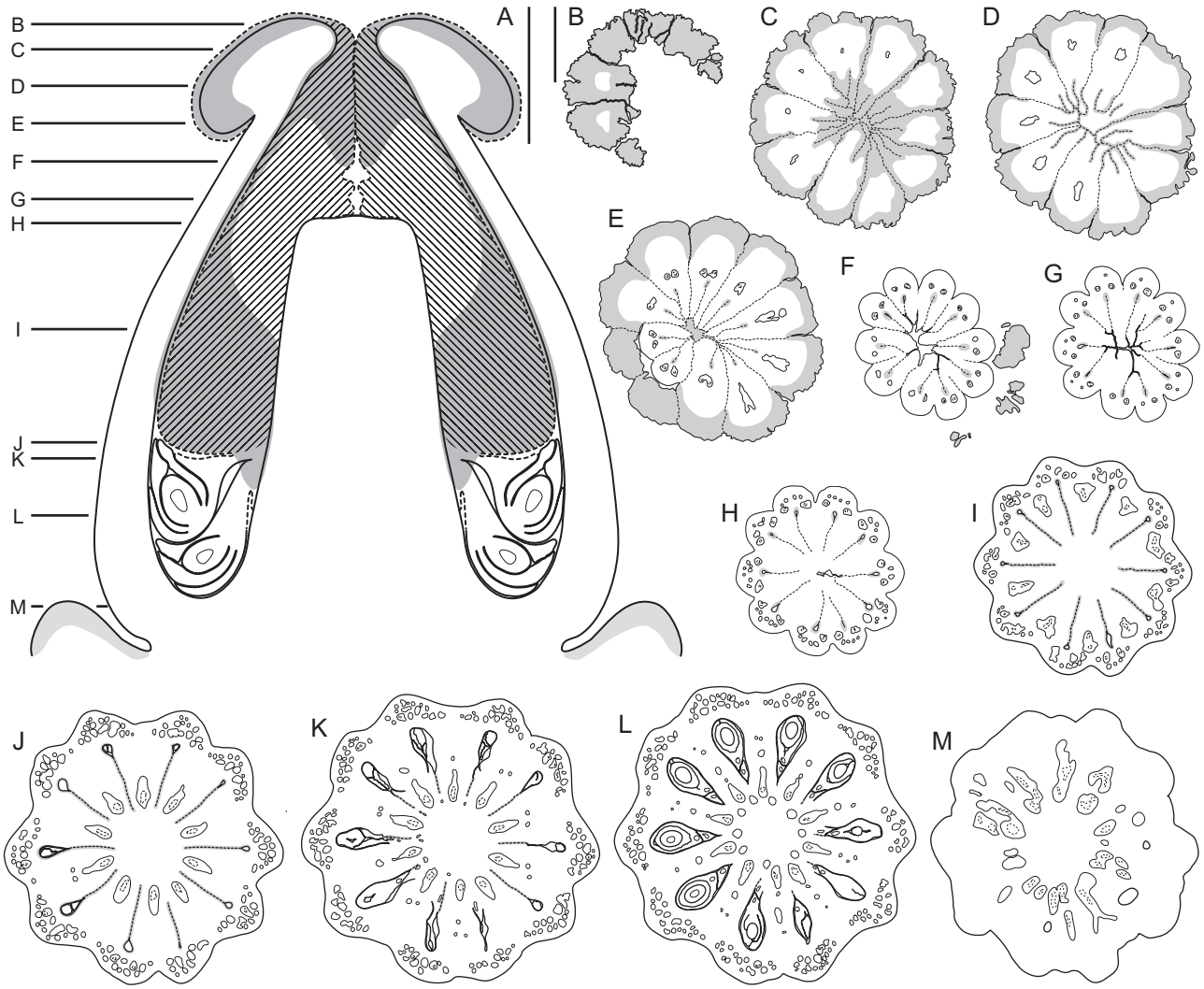


Figure 4. *Beiselia mexicana* (Burseraceae). Anthetic gynoecium. A, schematic median longitudinal section. B–M, transverse section series. B–E, apocarpous zone, stigmatic head formed by postgenitally united carpel tips (stigmas forming a compitum). F, transition between apocarpous and symplicate zone. G, short symplicate zone. H–M, synascidiate zone, ovary. H–I, above locules. J–L, locules with two superposed, pendant, antitropous, bitegmic ovules. M, below most of the locules. Scale bars, 500 μm.

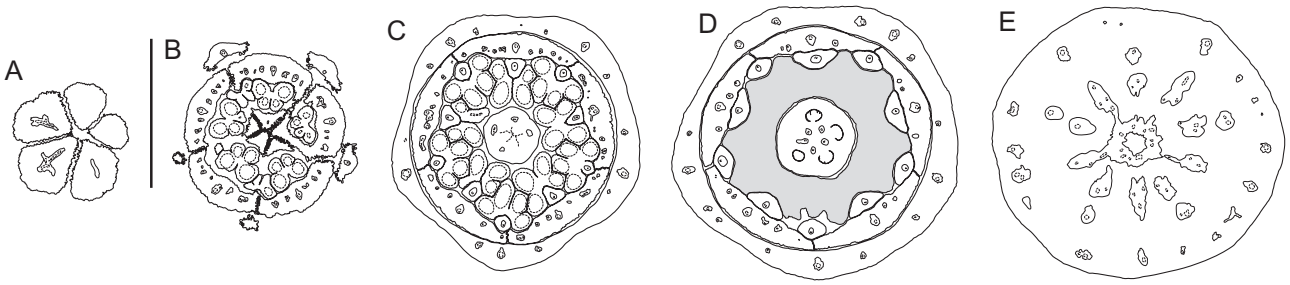


Figure 5. *Protium obtusifolium* (core Burseraceae). Male flower bud, transverse section series, from top, downwards. A, distal zone, petals valvate. B, sepals, petals valvate with tips bent inwards in centre, surrounded by anthers. C, synsepalous zone, petals valvate with oblique margins, gynoecium reduced, symplicate zone. D, synascidiate zone, locules with a single reduced ovule in median position. E, floral base. Scale bar, 1 mm.

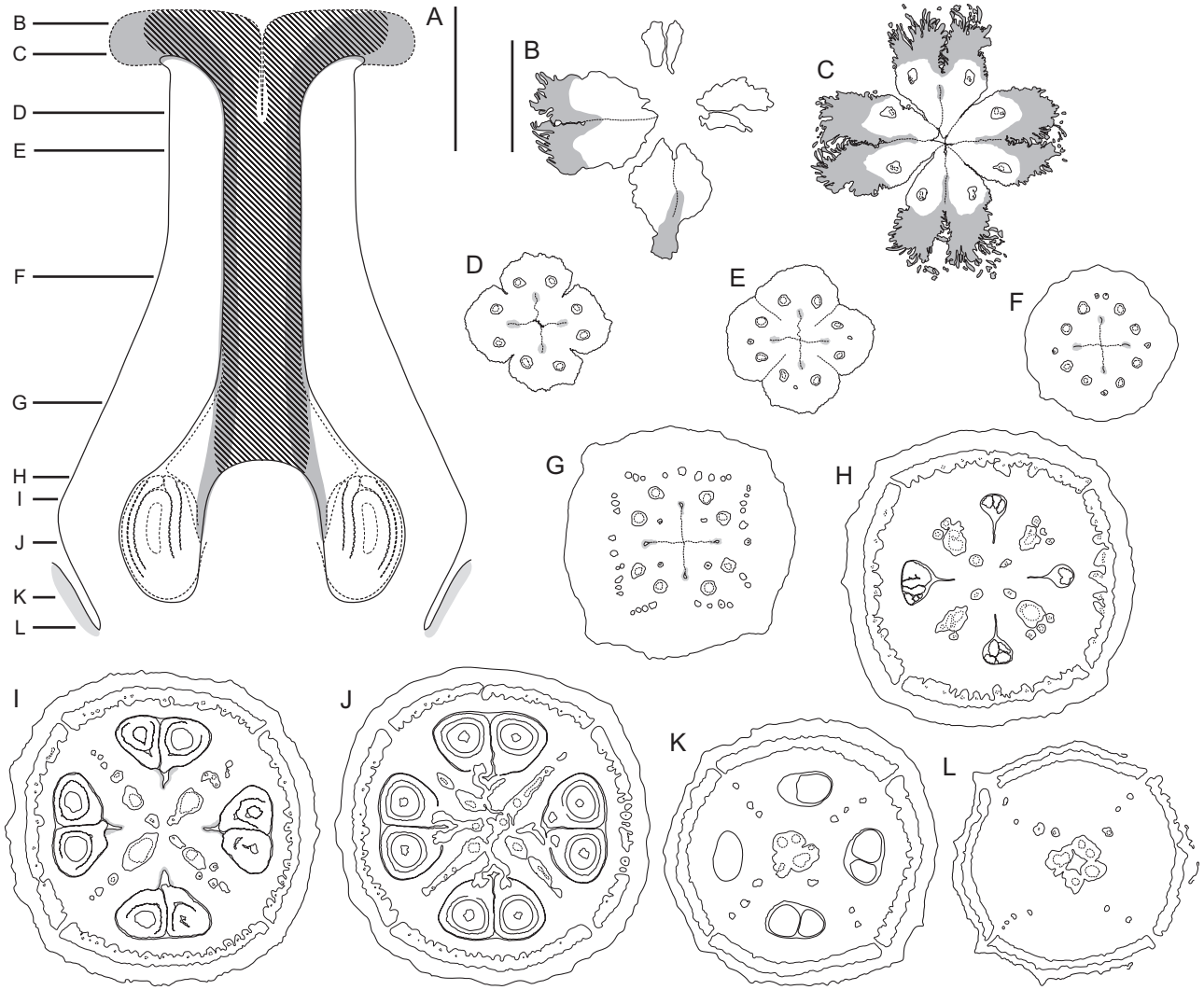


Figure 6. *Protium morii* (core Burseraceae). Anthetic gynoecium. A, schematic median longitudinal section. B–L, transverse section series. B–C, apocarpous zone, stigmatic head formed by carpel tips. B, carpel tips, reflexed and contiguous (stigmas not clearly forming a compitum). C, carpel tips, postgenitally united. D–G, symplicate zone. H–K, synascidiate zone, with two collateral, pendant, antitropous, bitegmic ovules per locule. L, ovary base, below locules. Scale bars, 500 μm.

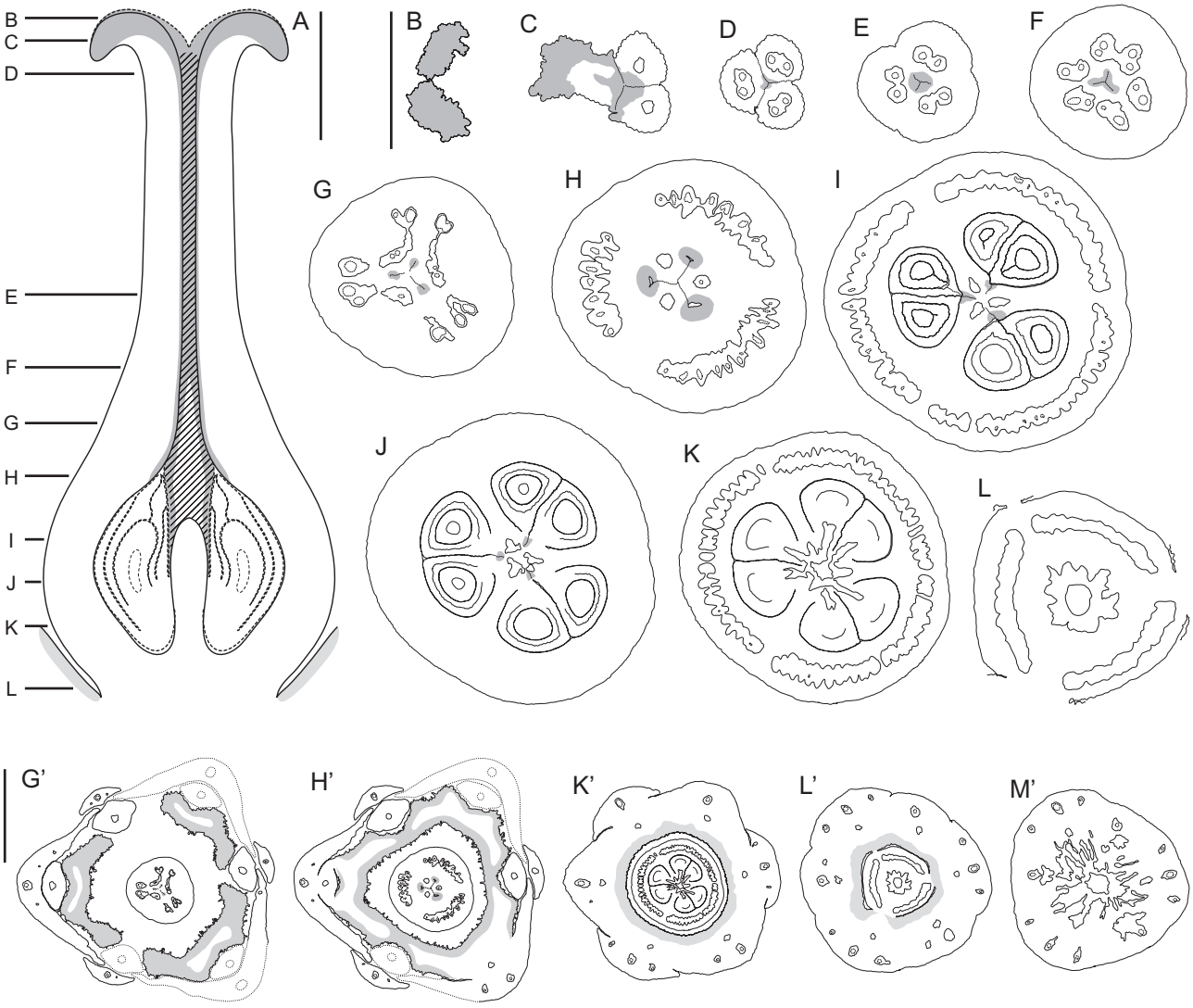


Figure 7. *Bursera* sp. (core Burseraceae). Anthetic gynoecium and flower base. A, schematic median longitudinal section. B–L, transverse section series. B–D, apocarpous zone. B–C, stigmatic head formed by postgenitally united, reflexed carpel tips (stigmas forming a compitum). D, postgenitally united styles forming an internal compitum. E–H, symplicate zone. E–F, with internal compitum. I–K, synascidiate zone, ovary with two collateral, pendant, antitropous, bitegmic ovules per locule. L, ovary base, below locules. G′–M′, floral cup, at levels corresponding to gynoecium sections (except for M′, which is below the gynoecium). G′, sepals, petals, stamen bases, intrastaminal nectary disc with antepetalous lobes (missing parts reconstructed with dotted line). H′, floral cup, formed by united petal and stamen bases, and nectary disc,. K′, floral cup, sepal margins still free. L′, gynoecium base. M′, floral base. Scale bars, 500 μm (A–M); 1 mm (G′–M′).

The micropyle is thus formed by the inner integument only and, because the ovules are superposed, the micropyle of the upper ovule is in close contact with the base of the stylar canal, whereas that of the lower ovule faces the dorsal wall of the locule (Figs 4A, 48A, B).

Anatomy: Vascular bundles comprise a more or less conspicuous ventral xylem and a dorsal resin canal, except for the ovule bundle (Figs 3, 4). Sepal bases have a median vascular bundle and two smaller lateral ones, which form synlaterals in the synsepalous region. Further up, the lateral bundles may branch, forming one or two additional, minor lateral bundles (Fig. 3B–D). Petal bases have a single main median vascular trace associated further up with one to two pairs of lateral bundles. In addition, each lateral bundle branches variously into three to four pairs of additional, much smaller bundles, which are intercalated between the three or five main bundles

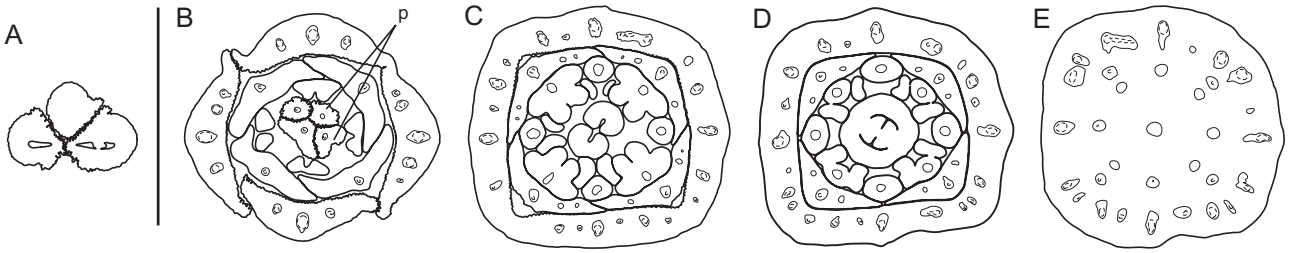


Figure 8. *Commiphora caudata* (core Burseraceae). Female flower bud, transverse section series. A, distal zone, petal tips valvate bent inwards. B, sepals valvate–imbricate, petals contort with valvate tips (p) bent inwards in centre, surrounded by antesepalous anthers. C, synsepalous zone (calyx tube), antesepalous stamens larger than antepetalous ones, two antepetalous carpel tips. D, petal aestivation open at the base, gynoecium symplicate zone. E, floral base, below floral cup. Scale bar, 1 mm.

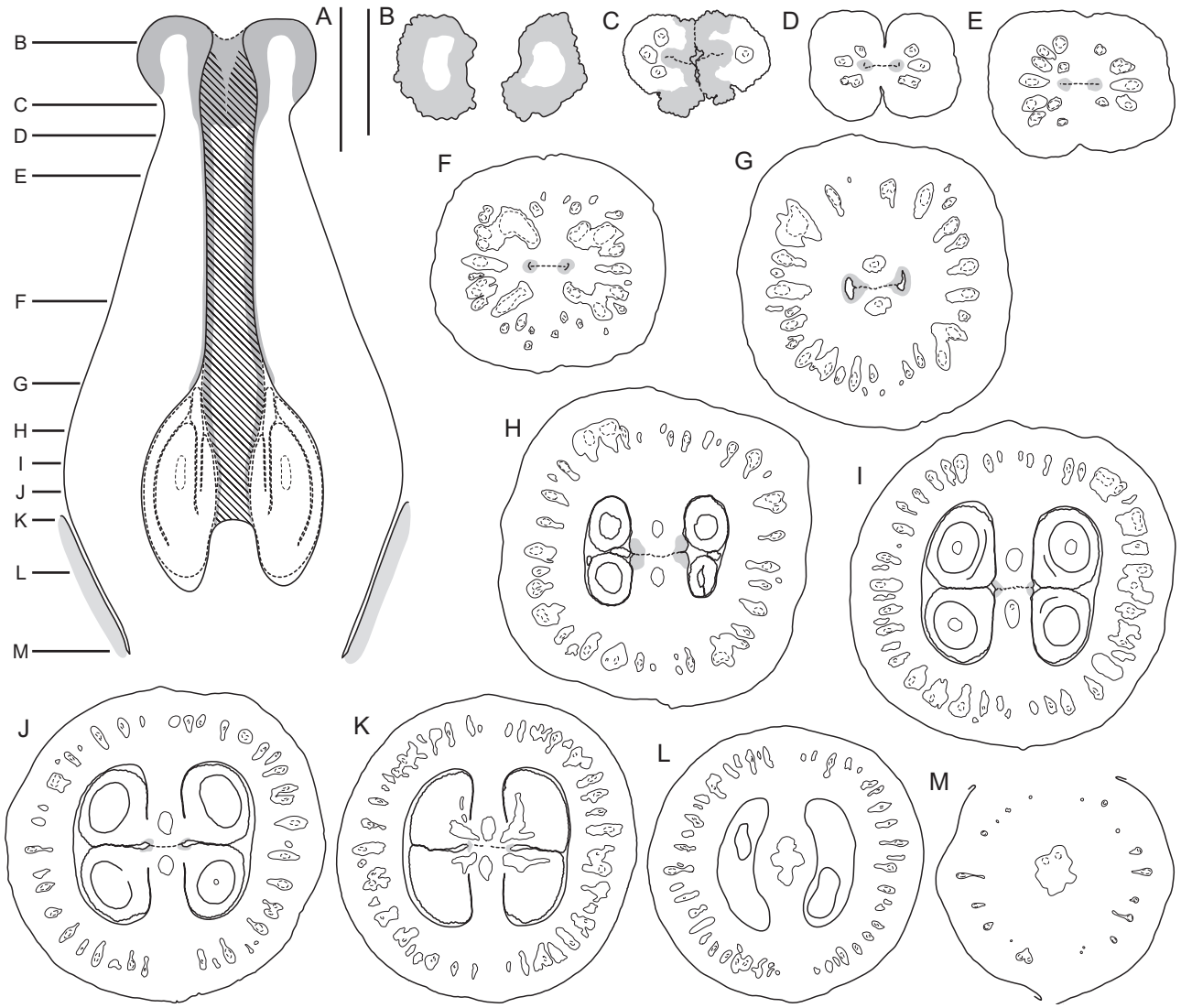


Figure 9. *Commiphora caudata* (core Burseraceae). Anthetic gynoecium. A, schematic median longitudinal section. B–M, transverse section series. B–C, apocarpous zone. B, carpel tips, slightly reflexed. C, stigmatic head formed by postgenitally united carpel tips (stigmas forming a compitum). D–J, symplicate zone. K–L, synascidiate zone. H–K, ovary with two collateral, pendant, antitropous, bitegmic ovules per locule. L, ovary at base of ovules. M, ovary base, below locules. Scale bars, 500 μm.

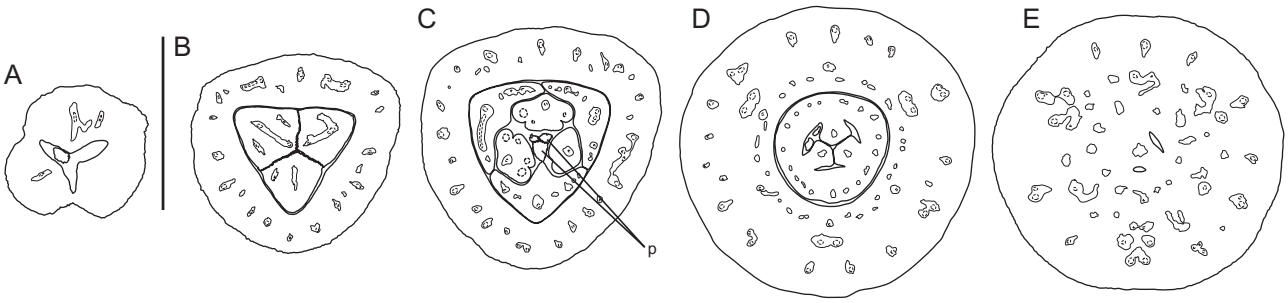


Figure 10. *Canarium caudatum* (core Burseraceae). Female flower bud, transverse section series. A, distal zone, sepals, congenitally united. B, synsepalous zone, petals valvate. C, petals valvate with oblique margins, and tips (p) bent inwards in centre, surrounded by antesepalous (sterile) anthers. D–E, floral cup. D, gynoecium symplicate zone. E, floral base, two locules still visible. Scale bar, 1 mm.

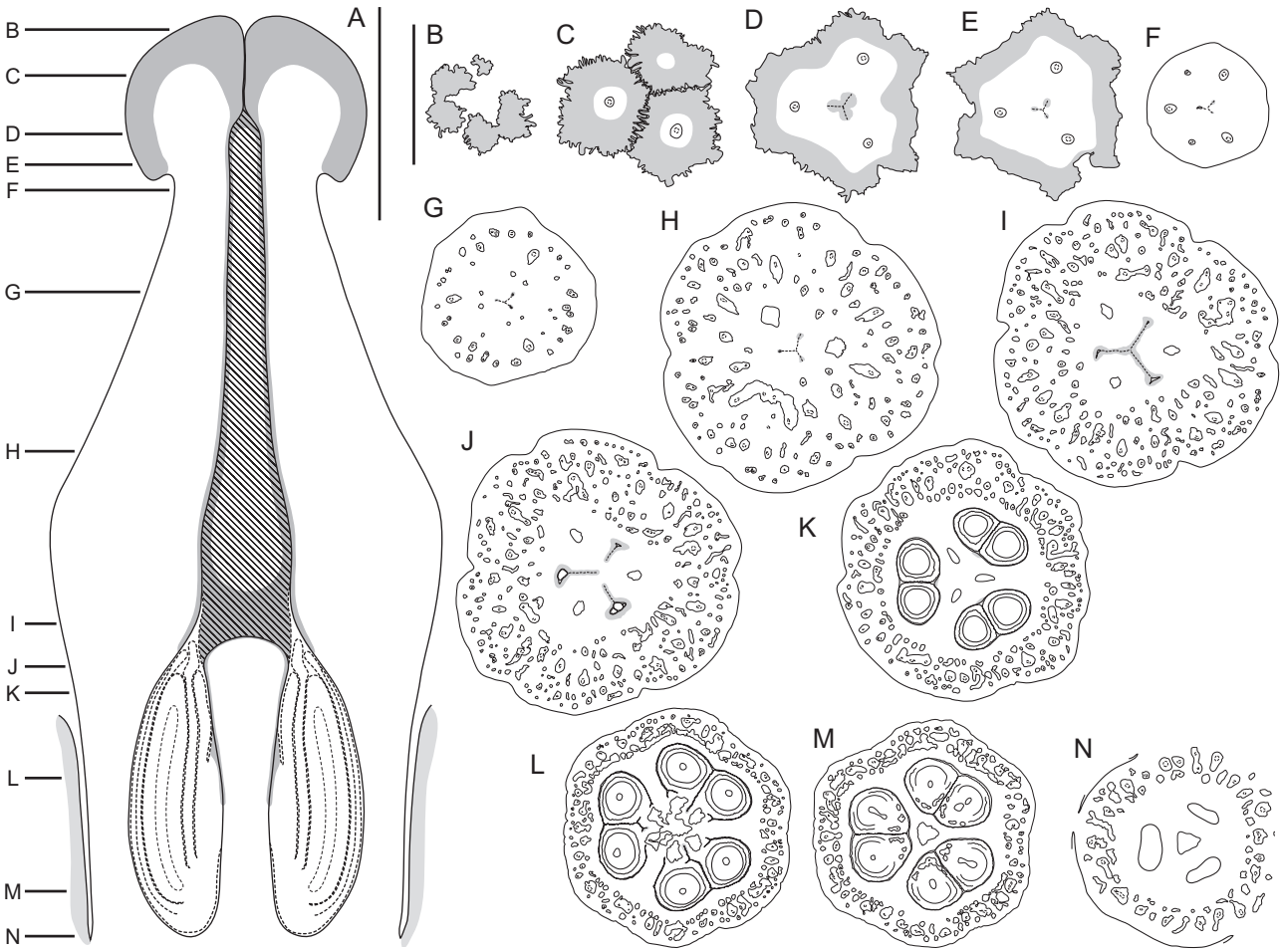


Figure 11. *Canarium caudatum* (core Burseraceae). Anthetic gynoecium. A, schematic median longitudinal section. B–N, transverse section series. B–E, stigmatic head formed formed by carpel tips . B–C, apocarpous zone. B, carpel tips. C, carpel tips contiguous (stigmas forming a compitum). D–J, symplicate zone (potential intragynoecial compitum in I). K–N, synascidiate zone. K–L, ovary, two collateral, pendant, antitropous, bitegmic ovules per locule. N, ovary base, below ovules. Scale bars, 1 mm.

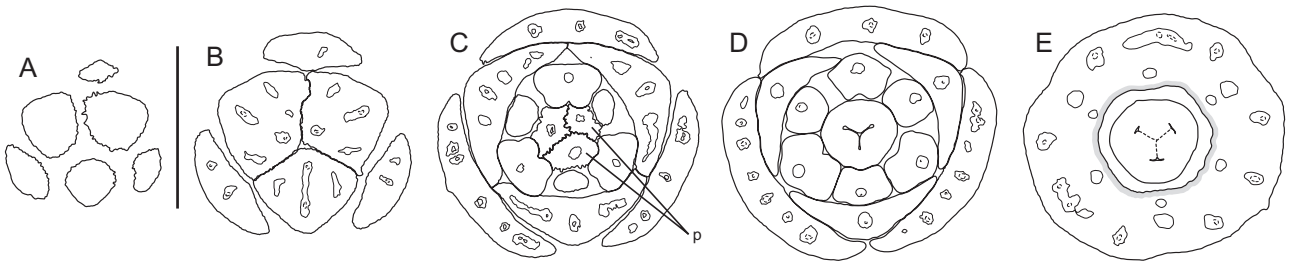


Figure 12. *Santiria* cf. *apiculata* (core Burseraceae). Female flower bud, transverse section series. A, distal zone, sepal and petal tips. B, petal tips valvate bent inwards. C, petals valvate with tips bent inwards in centre (p), surrounded by anthers, antesepalous anthers larger than antepetalous ones. D, petal aestivation open at the base, stamens, gynoecium symplicate zone. E, floral cup, gynoecium upper end of locules. Scale bar, 500 μm.

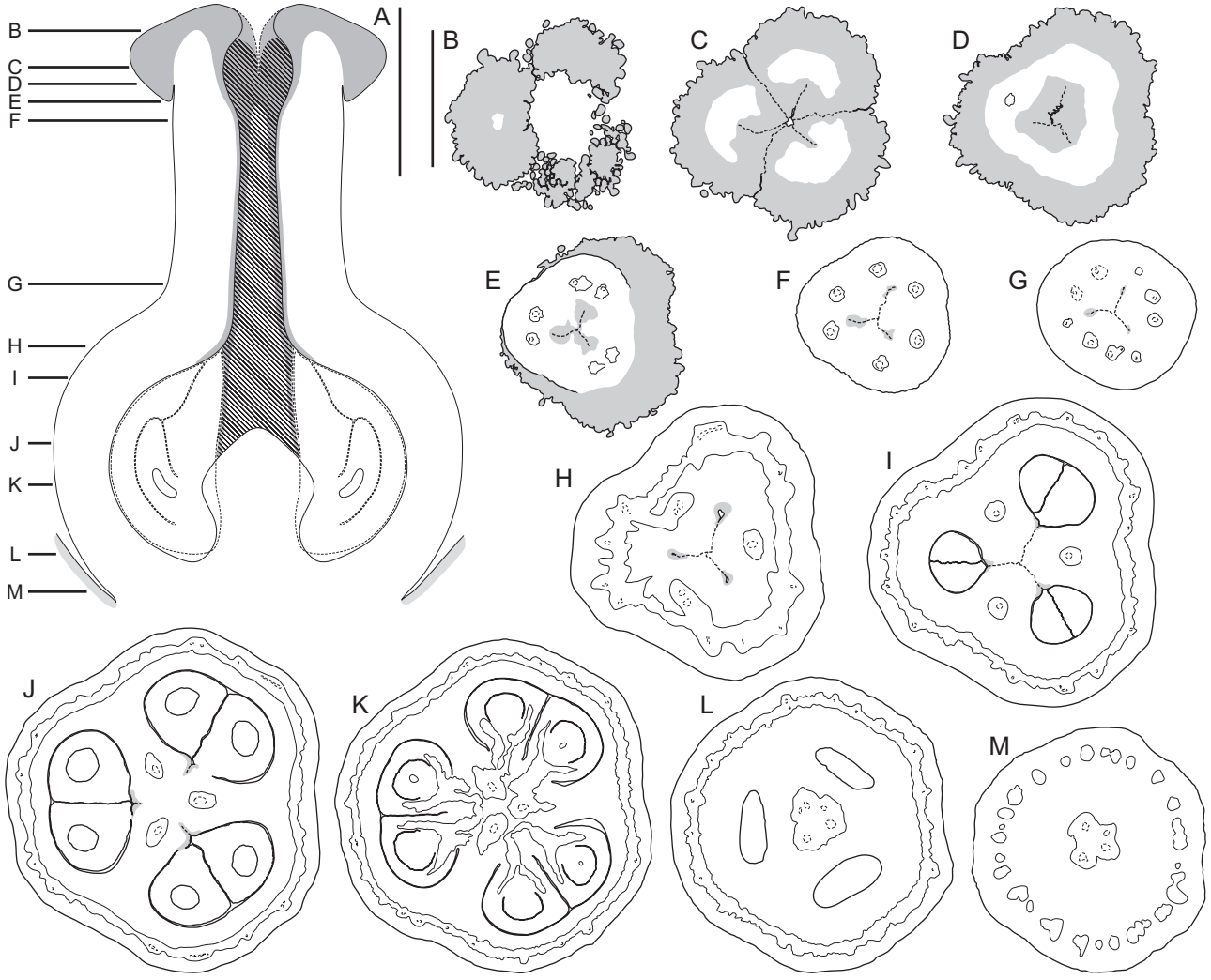


Figure 13. *Santiria* cf. *apiculata* (core Burseraceae). Anthetic gynoecium. A, schematic median longitudinal section. B–M, transverse section series. B–E, stigmatic head formed by carpel tips. B–C, apocarpous zone. C, carpel tips postgenitally united (stigmas forming a compitum). D–I, symplicate zone. J–L, synascidiate zone. I–K, ovary, two collateral, pendant, antitropous, unitegmic ovules per locule. L, ovary, below ovules. M, ovary base, below locules. Scale bars, 500 μm.

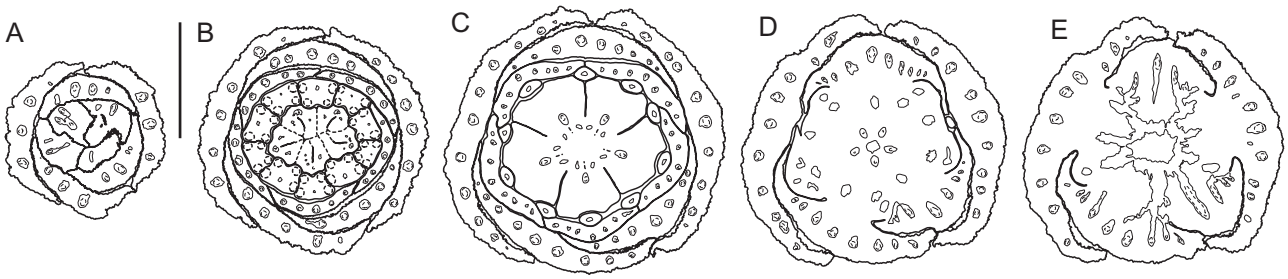


Figure 14. *Dracontomelon dao* (Anacardiaceae, Spondiadoideae). Female flower bud, transverse section series. A, distal zone, sepals quincuncial, petals with tips inflexed inwards. B, petals cochlear, antesepalous stamens larger than antepetalous ones, carpels postgenitally united. C, gynoecium synascidiate zone. D–E, floral base, sepal margins still free. Scale bar, 1 mm.

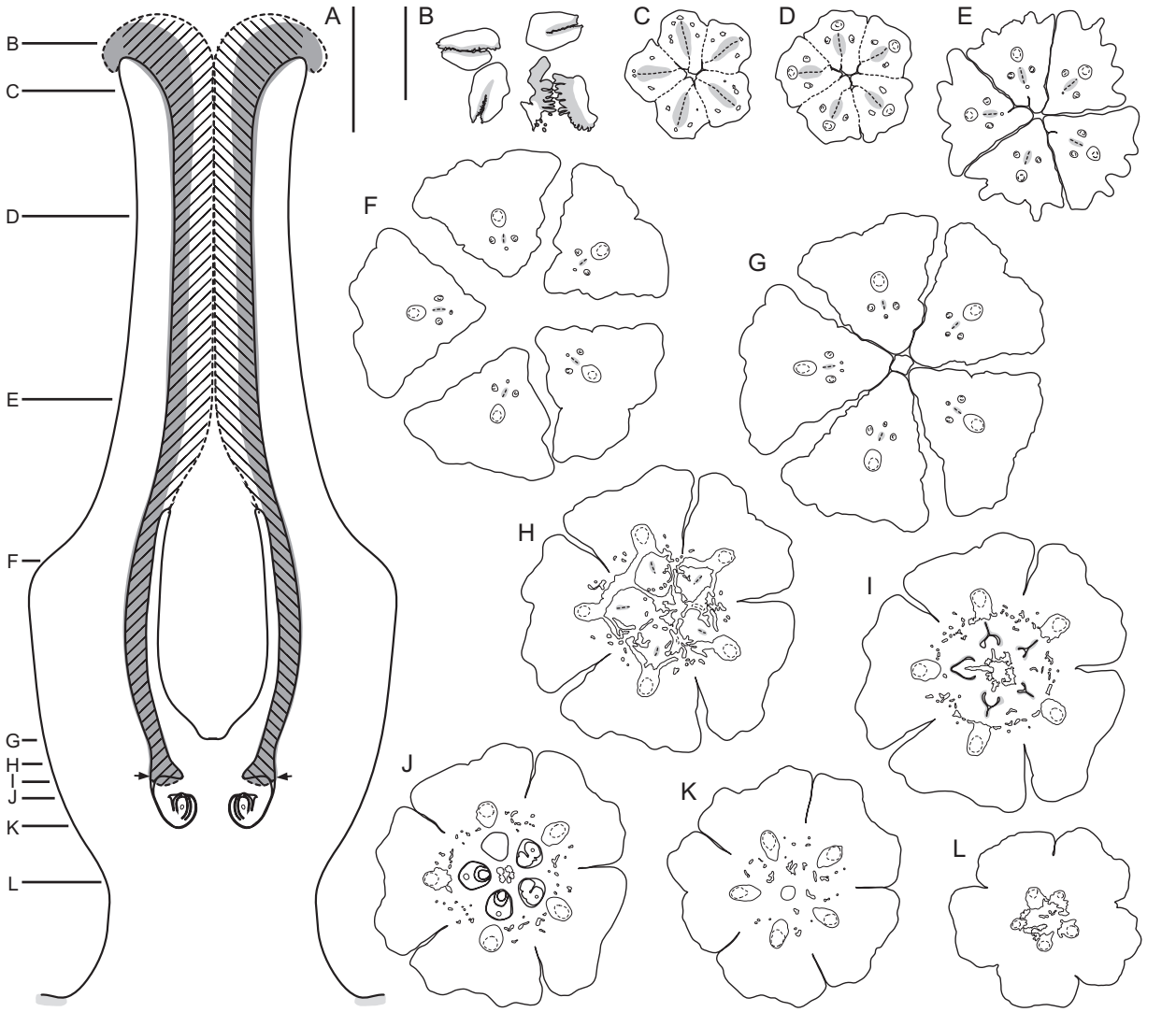


Figure 15. *Dracontomelon dao* (Anacardiaceae, Spondiadoideae). A, schematic median longitudinal section. B–L, transverse section series. B–G, apocarpous zone. B, carpels tips, plicate and reflexed. C–D, carpels postgenitally united. E–G, carpels, appearing ascidiate. G, style bases, former floral apex in centre. H–K, synascidiate zone, ovary. H, above the locules. I–J, locules, with a single median, apical, anatropous, syntropous, bitegmic ovule per locule. I, zone of *ponticulus* [arrows in (A)]. K, below locules. L, gynophore. Scale bars, 1 mm.

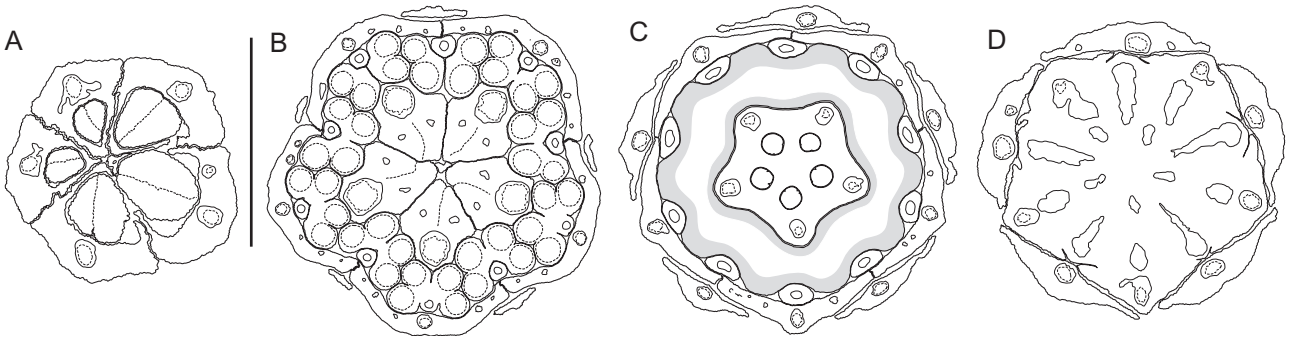


Figure 16. *Spondias dulcis* (Anacardiaceae, Spondiadoideae). Flower bud, transverse section series. A, distal part, petal valvate tips hooded, surrounding carpel tips. B, sepals, petals valvate, antesepalous stamens slightly larger than antepetalous ones, gynoecium apocarpous zone. C, nectary disc with lobes alternating with stamen bases, gynoecium synascidiate zone. D, floral base. Scale bar, 1 mm.

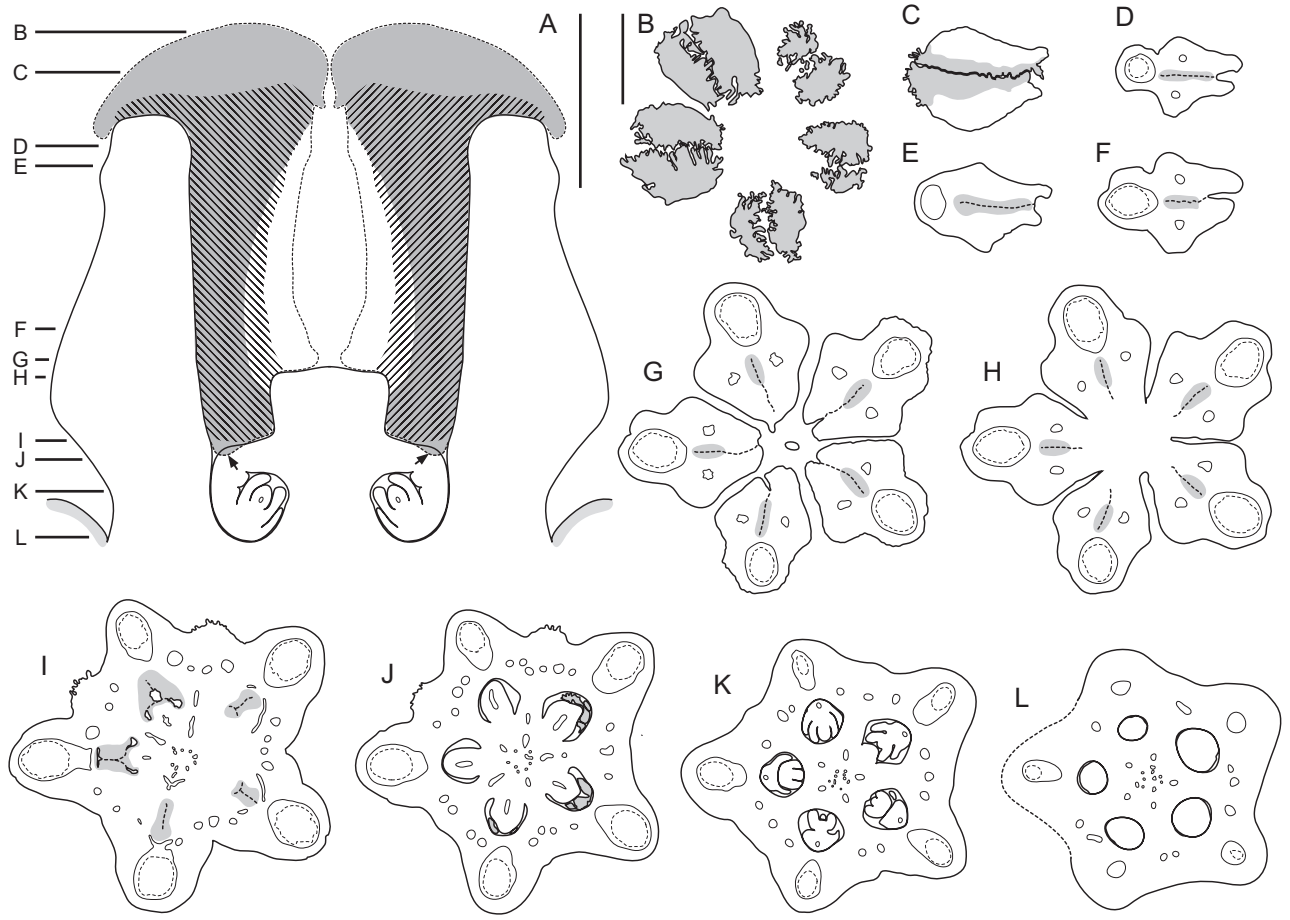


Figure 17. *Spondias dulcis* (Anacardiaceae, Spondiadoideae). Anthetic gynoecium. A, schematic median longitudinal section. B–L, transverse section series. B–G, apocarpous zone (in C–F only one of the five carpels shown). B–C, stigmas. D–G, styles. G, former floral apex in the centre. H–L, synascidiate zone, ovary. H, above locules. I–L, locules, with a single median, apical, anatropous, syntropous, bitegmic ovule per locule. I–J, zone of *ponticulus* [arrows in (A)], with pollen tube transmitting tract (PTTT) projections in the ceiling of the locule at the base of stylar canals. Scale bars, 500 μm.

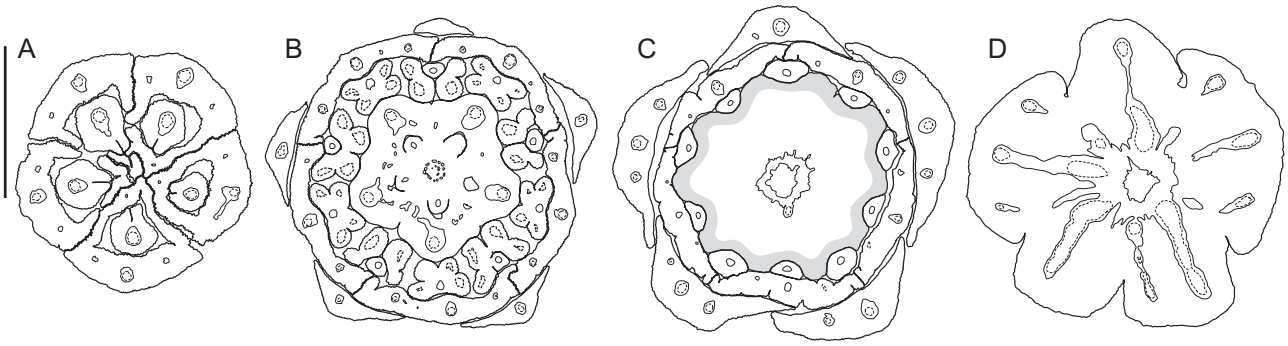


Figure 18. *Spondias purpurea* (Anacardiaceae, Spondiadoideae). Female flower bud, transverse section series. A, distal part, petal valvate tips hooded, surrounding carpel tips. B, sepals, petals valvate (with asymmetric margins), antesepalous stamens slightly larger than antepetalous ones, gynoecium synascidiate zone. C, sepals quincuncial, outermost two larger than inner ones, petals more or less valvate, nectary disc with lobes alternating with stamen bases. D, floral base, sepal margins still free. Scale bar, 1 mm.

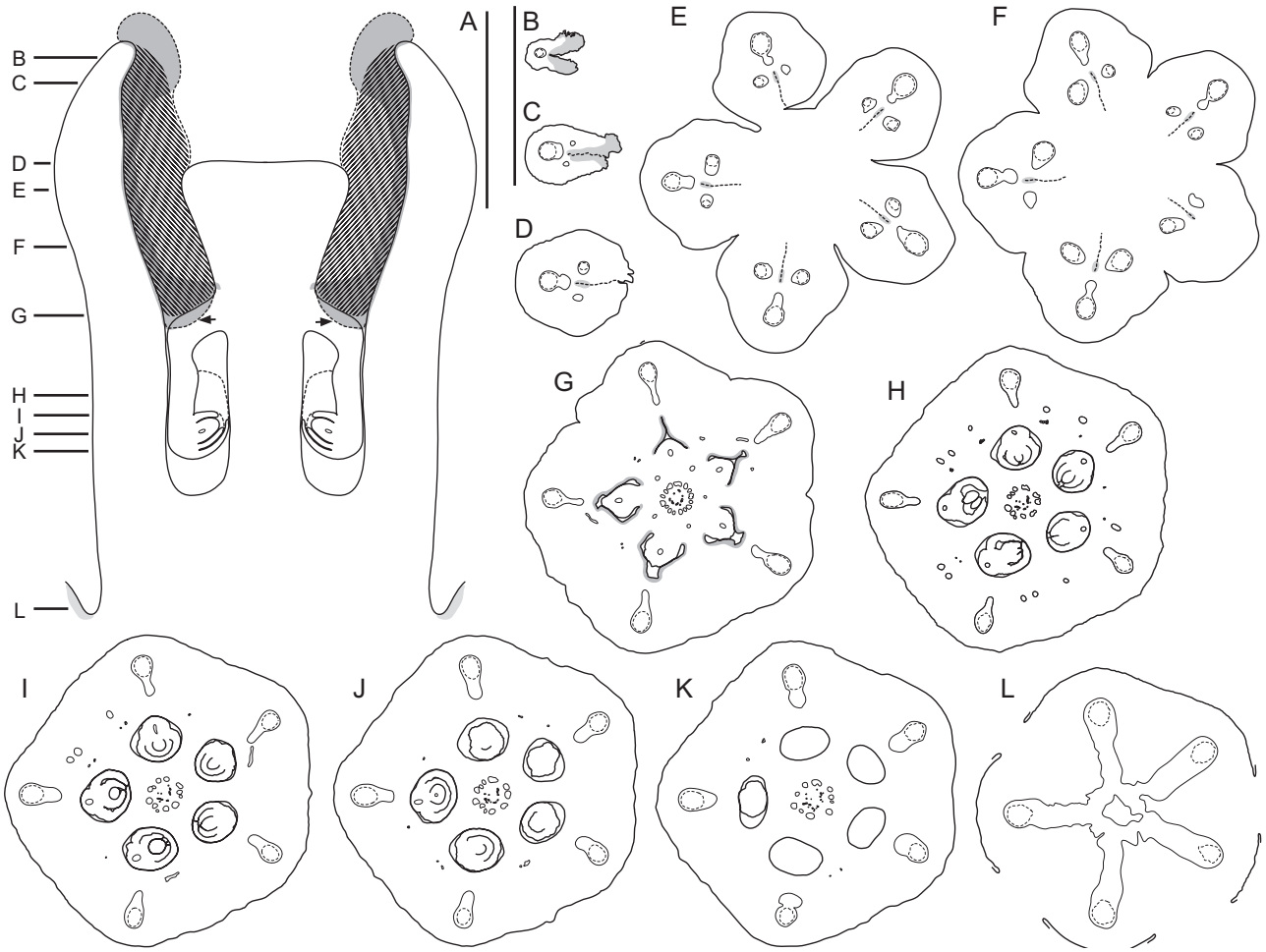


Figure 19. *Spondias purpurea* (Anacardiaceae, Spondiadoideae). Anthetic gynoecium. A, schematic median longitudinal section. B–L, transverse section series. B–D, apocarpous zone (only one of the five carpels shown). E–K, synascidiate zone, ovary. E–F, above locules. G–K, locules, with a single median, apical, anatropous, syntropous, bitegmic ovule. G, zone of *ponticulus* [arrows in (A)]. L, below locules. Scale bars, 1 mm.

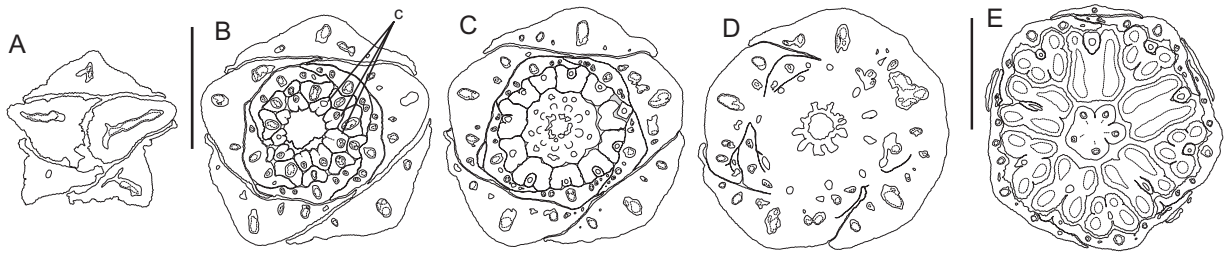


Figure 20. *Pleiogynium solandri* (Anacardiaceae, Spondiadoideae). A–D, female flower bud, transverse section series. A, distal part, sepals quincuncial. B, petals cochlear, anthers with resin canal, ovary roof in centre, surrounded by nine free carpel tips (c). C, antesepalous stamens larger than antepetalous ones, gynoecium syncarpous zone, with nine young ovules. D, floral base, sepal margins still free. E, male flower bud, transverse section. Petals cochlear, antesepalous anthers inflexed, reduced gynoecium synascidiate zone. Scale bars, 1 mm.

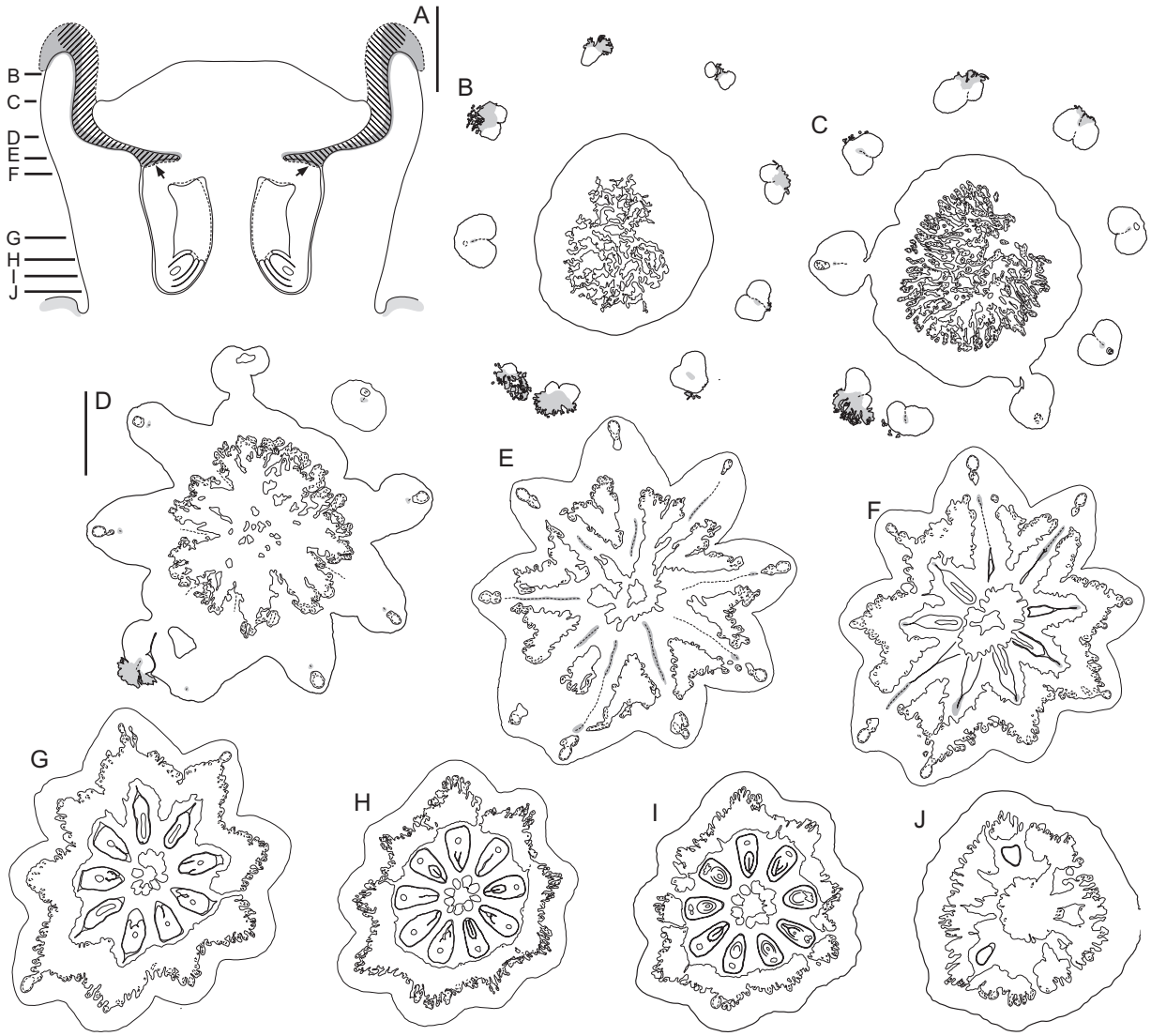


Figure 21. *Pleiogynium solandri* (Anacardiaceae, Spondiadoideae). Anthetic gynoecium. A, schematic median longitudinal section. B–J, transverse section series. B, apocarpous zone, carpel tips plicate, ovary roof in centre. C, transition from apocarpous to synascidiate zone. D–J, synascidiate zone, ovary. D–E, above locules. E–F, zone of *ponticulus* [arrows in (A)]. F–I, locules, with a single median, apical, anatropous, syntropous, bitegmic ovule per locule. J, below ovules. Scale bars, 500 μm.

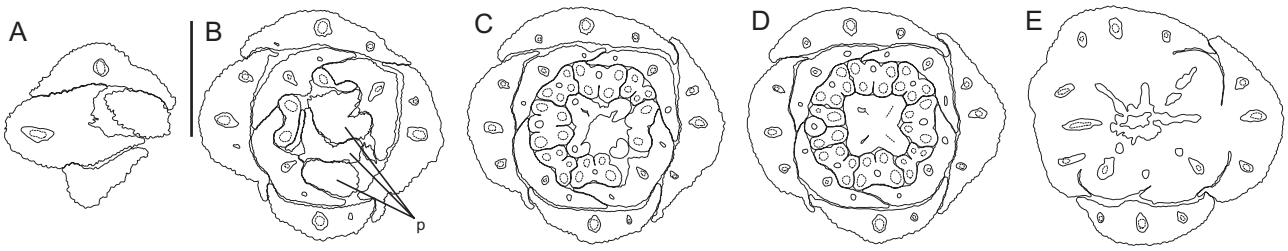


Figure 22. *Pseudospondias microcarpa* (Anacardiaceae, Spondiadoideae). Male flower bud, transverse section series. A, distal part, sepals imbricate. B, petals imbricate with tips (p) bent inwards in centre, antesepalous anthers. C, antesepalous stamens larger than antepetalous ones (one stamen not visible), reduced gynoecium, transition from apocarpous to synascidiate zone. D, reduced gynoecium synascidiate zone. E, floral base, sepal margins still free. Scale bar, 1 mm.

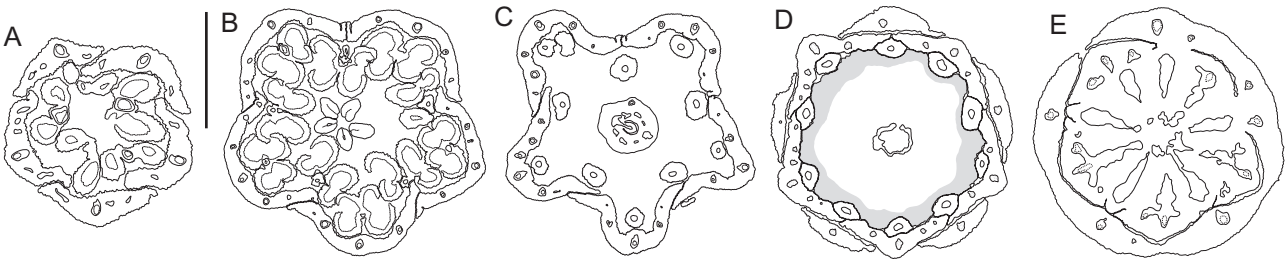


Figure 23. *Tapirira sp*. (Anacardiaceae, Spondiadoideae). Male flower bud, transverse section series. A, distal part, petals quincuncial, antesepalous anthers, with resin canal. B, petal aestivation labile (valvate and imbricate), reduced gynoecium apocarpous zone. C, antesepalous filaments larger than antepetalous ones, gynoecium pseudomonomerous, syncarpous zone, with fertile carpel antepetalous. D, sepals, nectary disc with lobes alternating with stamen bases. E, floral base, short synsepalous zone, sepal flanks still free from floral base. Scale bar, 500 μm.

(Fig. 3A–D). Stamens or staminodes have a single vascular bundle, in which the xylem is not conspicuously differentiated but the resin canal is well developed (Fig. 3C). In the carpels, a median dorsal vascular bundle is present in the stigmatic region (Fig. 4C, D). Further down, it splits into two smaller collateral branches, which become more lateral with regard to the ventral slit just above the ovary (Fig. 4E–G). In the ovary, an arc of smaller vascular bundles extends into the dorsal region (Fig. 4H–L). In the synascidiate zone, the laterals of adjacent carpels form synlateral bundles (Fig. 4I). The synlaterals converge toward the central part of the ovary and are unusual in that they have dorsal xylem and a large ventral resin canal (Fig. 4J–M). Below the level of the placentae, each synlateral bundle forms two branches, which fuse with the branches of the adjacent synlaterals. Together, they form a median ventral vascular bundle, which further up splits into two ovular bundles (Fig. 4K, L). In the lower part of the ovary, below the locules, dorsal, median ventral and synlateral bundles converge toward the central region of the gynoecium and merge to form a ring of vascular tissue (Fig. 4M).

Histology: Stomata are present on the dorsal side of the sepals and carpels except for the stigmatic region. Hairs are present only on the perianth (Fig. 40A). They are either unicellular (sepals and petals) or multicellular, with a uniseriate stalk and glandular head (petals). The nectary disc has a smooth surface and contains nectar pores. Striate cuticular epidermal ornamentation is more or less conspicuous on the floral organs and on non-glandular hairs, except for the gynoecium and nectary disc.

Protium morii (female) (Figs 6, 40E, F, 44B, 45D–F) and *P. obtusifolium* (male) (Figs 5, 40G–I, 43B, B′, 44C) (Burseraceae)

Morphology: The flowers are morphologically bisexual, tetramerous (*P. morii*) or pentamerous (*P. obtusifolium*), isomerous and obdiplostemonous (Figs 5, 40E–I). The sepals are congenitally united for most of their length (*P. morii*), or only shortly (*P. obtusifolium*), and their tips have an open aestivation. Petal aestivation is valvate, with the united petal tips bent inwards and shortly open basally (Fig. 5C, D). The corolla becomes longer than the calyx early in

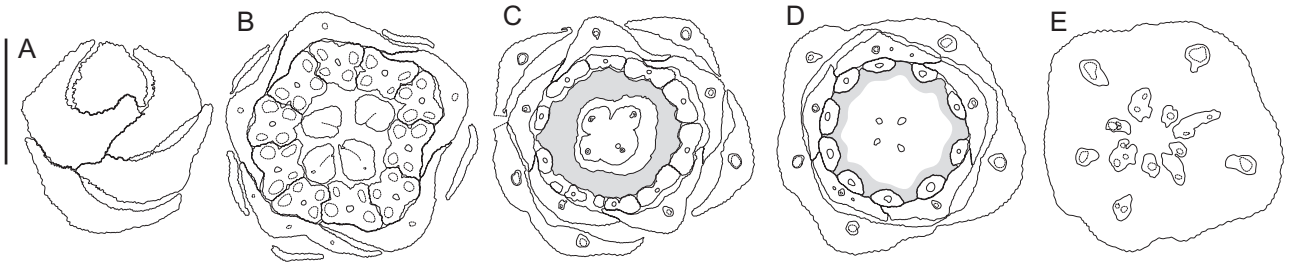


Figure 24. *Buchanania arborescens* (Anacardiaceae, Spondiadoideae). Female flower bud, transverse section series. A–C, petals cochlear, but arrangement of petal margins switching two times. A, distal part. B, antesepalous stamens slightly larger than antepetalous ones, gynoecium apocarpous zone. C, synsepaly beginning, gynoecium synascidiate zone. D, synsepalous zone, nectary disc with lobes alternating with stamen bases. E, floral base. Scale bar, 500 μm.

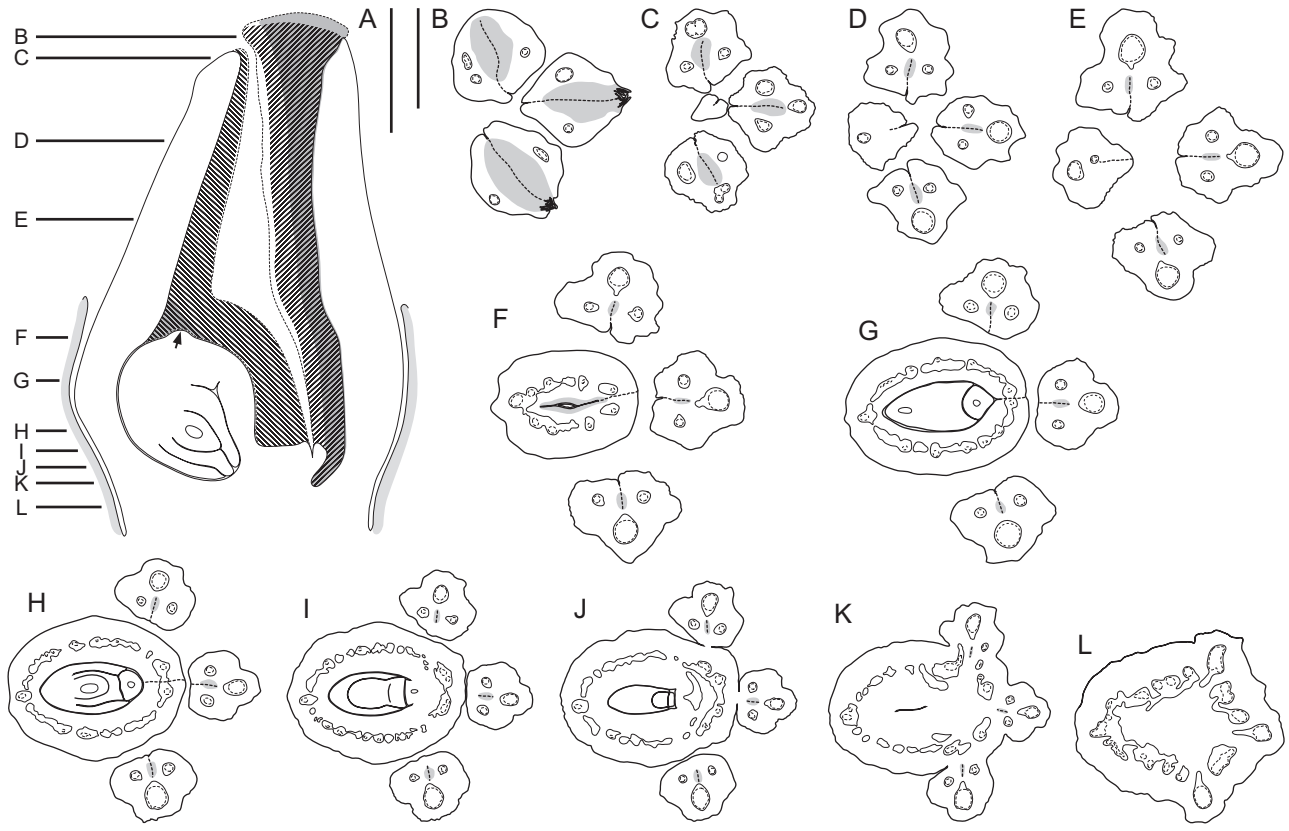


Figure 25. *Buchanania arborescens* (Anacardiaceae, Spondiadoideae). Anthetic gynoecium. A, schematic median longitudinal section. B–L, transverse section series. B–I, apocarpous zone, carpel tips plicate. B, stigmas of sterile carpels. C, tip of the fertile carpel lacking a stigma and styles of sterile carpels with pollen tube transmitting tract (PTTT). D–E, fertile carpel lacking a PTTT. F, above locule (of the fertile carpel), zone of *ponticulus* [arrow in (A)]. G–J, ovary, with a single median, basally inserted, anatropous, syntropous, bitegmic ovule. J–K, synascidiate zone. L, ovary base, below locule. Scale bars, 500 μm.

development and protects the reproductive organs in bud (Figs 5A–C, 40G). Postgenital cohesion of the valvate petal margins is formed by unicellular and uniseriate multicellular (up to 4-celled) papillae and striate cuticular ornamentation. At anthesis, the sepal tips are obtuse. The petals are acute and erect (*P. morii*) or reflexed at mid-length (*P. obtusifolium*) (Fig. 40E, H, I). Their tips retain the inward bend that they had in bud (Figs 5A, B, 40F–I). The reproductive organs are shorter than the petals and remain partly hidden by the corolla (*P. morii*, Fig. 40E, F).

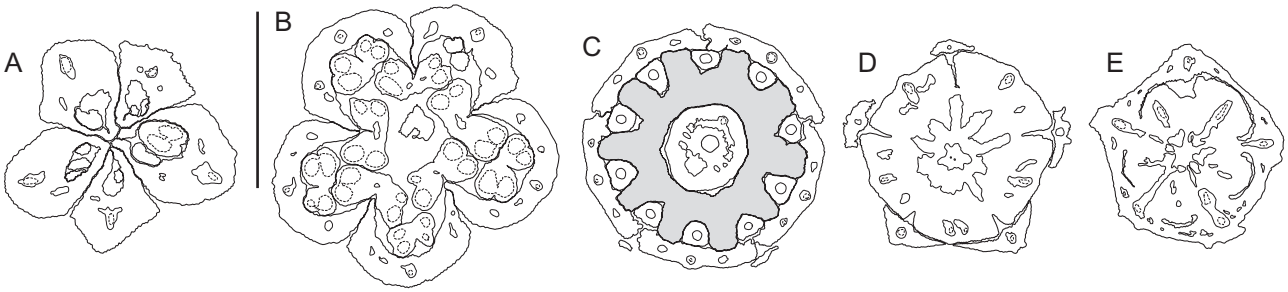


Figure 26. *Solenocarpus philippinensis* (Anacardiaceae, Spondiadoideae). Flower bud, transverse section series. A, distal part, petal valvate tips hooded, surrounding thecae tips of two adjacent antesepalous anthers. B, petals valvate, tip of the gynoecium in centre. C, petals, nectary disc with lobes alternating with stamen bases and surrounding ovary. D, floral base, sepal tips. E, synsepalous zone. Scale bar, 1 mm.

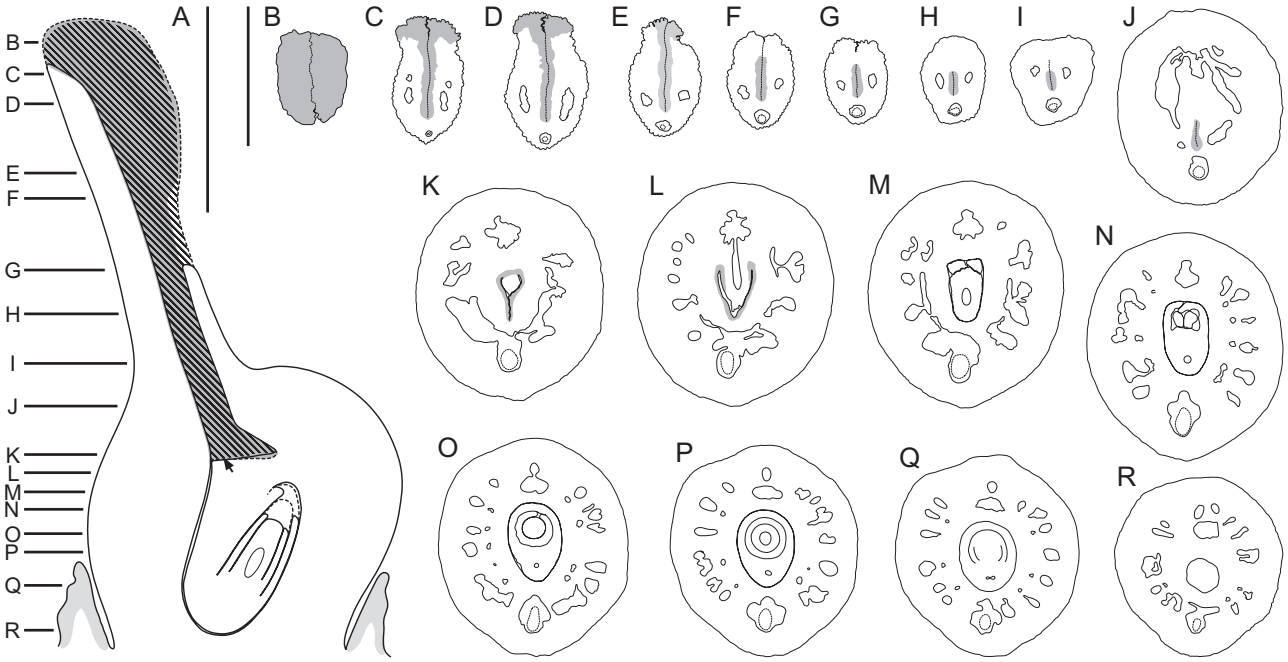


Figure 27. *Solenocarpus philippinensis* (Anacardiaceae, Spondiadoideae). Anthetic gynoecium. A, schematic median longitudinal section. B–R, transverse section series. B–E, carpel plicate zone, stigma. F–R, carpel ascidiate zone. F, carpel cross-zone (transition from plicate to ascidiate zone). F–I, style. J–R, ovary. J–K, above locule. K–L, zone of *ponticulus* [arrow in (A)]. L–R, locule, with a single median, apical, anatropous, syntropous, bitegmic ovule. R, below ovule. Scale bars, 500 μm.

The antepetalous stamens appear slightly longer and larger than the antesepalous ones. All stamens have a broad flattened filament base, which becomes rounder and narrows towards the constricted tip and a slightly sagittate (*P. morii*, Fig. 44B) or X-shaped anther (*P. obtusifolium*, Fig. 43B, 44C). The anthers are basally dorsifixed (*P. morii*, Fig. 44B) or dorsifixed in the lower half (*P. obtusifolium*). They have a connective of medium (*P. morii*, Fig. 44B) thickness or a thin connective (*P. obtusifolium*, Figs 43B, 44C) and a dorsal and a deep ventral longitudinal furrow (Fig. 44B, C). Their dorsal side is broader than the ventral side and the anthers are slightly introrse (Fig. 44B, C). The dehiscence lines extend from the tip of the thecae down to their base (Fig. 43B′). In our material of *P. morii*, the anthers are devoid of pollen and the flowers are functionally female and, in that of *P. obtusifolium*, the gynoecium is more or less reduced and the flowers functionally male. A thick lobed intrastaminal nectary disc surrounds the ovary base (Figs 5D, 40G).

The syncarpous gynoecium is polysymmetric, with as many symmetry planes as the polysymmetric flower (Figs 5C, D, 40F, I). It has a superior ovary

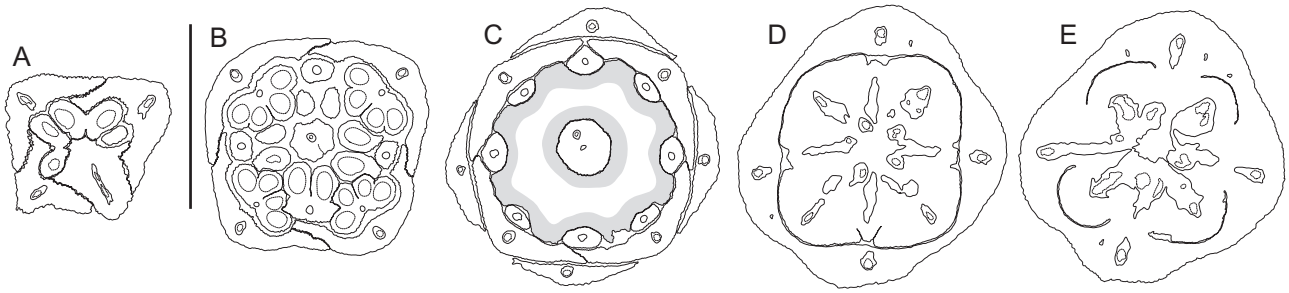


Figure 28. *Campnosperma squamatum* (Anacardiaceae, Spondiadoideae). Male flower bud, transverse section series. A, distal part, petal tips bent inwards, antesepalous anthers. B, petals imbricate, a single carpellode. C, sepals, petal aestivation imbricate–valvate, slightly open at the base, nectary disc with lobes alternating with stamen bases, sterile locule. D–E, floral base, synsepalous zone. E, sepal flanks still free from floral base. Scale bar, 1 mm.

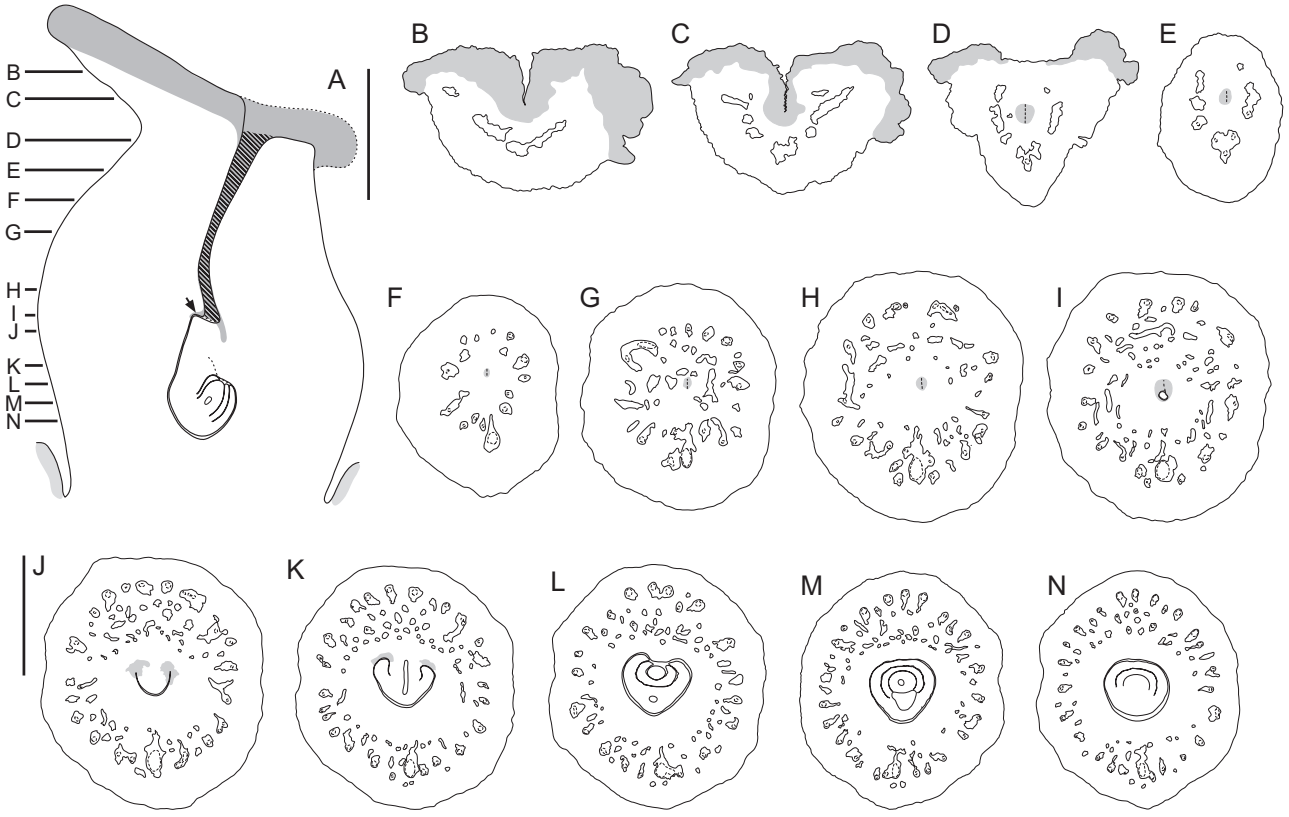


Figure 29. *Campnosperma squamatum* (Anacardiaceae, Spondiadoideae). Anthetic gynoecium. A, schematic median longitudinal section. B–N, transverse section series. B–C, carpel plicate zone, stigma flat and oblique. D–N, carpel ascidiate zone. D–H, above locule. I–N, ovary, with a single median, apical, anatropous, syntropous, bitegmic ovule. I–J, zone of *ponticulus* [arrow in (A)]. Scale bars, 500 μm.

(*P. morii*), lacks a distinct style and ends in a flat plate of four receptive carpel tips (stigmatic head) (Fig. 45D–F). Between the carpels, longitudinal furrows extend downwards from the stigmatic head (Fig. 45D, E); they end in the middle of the style (Fig. 6C–E) and, instead, slightly prominent ridges run along the ovary (Fig. 6F–L). The gynoecium is of angiospermy type 3 or 4 (Fig. 6). It is synascidiate at least up to mid-length of the ovary (Fig. 6A, H–L) and symplicate up to the base of the stigmatic head (Fig. 6A, C–G). There, it is apocarpous and each stigmatic branch corresponds to the plicate and slightly reflexed tip of a carpel (Fig. 6A, B). Each stigmatic branch is bilobed with a ventral furrow and is covered with uniseriate multicellular papillae (Fig. 6B, C). At anthesis, it is covered with secretion (Fig. 45E, F).

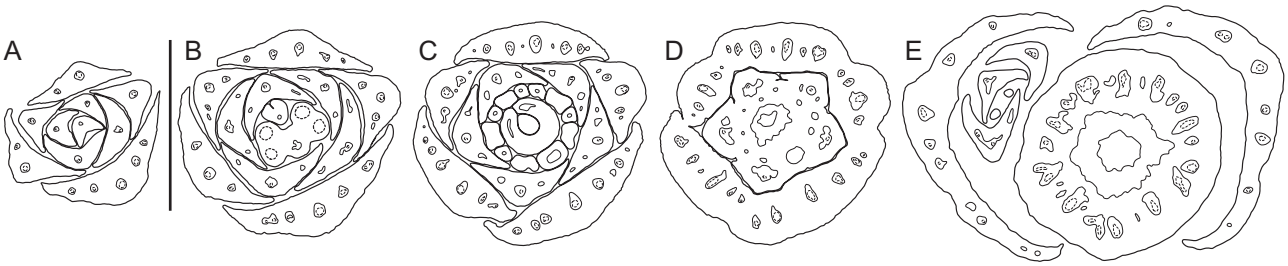


Figure 30. *Anacardium occidentale* (Anacardioideae, Anacardiaceae). Young flower bud, transverse section series. A, distal zone, sepals quincuncial. B, petals cochlear, the fertile stamen and single carpel on the radius of the first sepal. C, antesepalous staminodes larger than antepetalous ones, carpel plicate zone with a single ovule. D, synsepalous zone. E, floral base, two prophylls, flower bud in the axil of one prophyll. Scale bar, 1 mm.

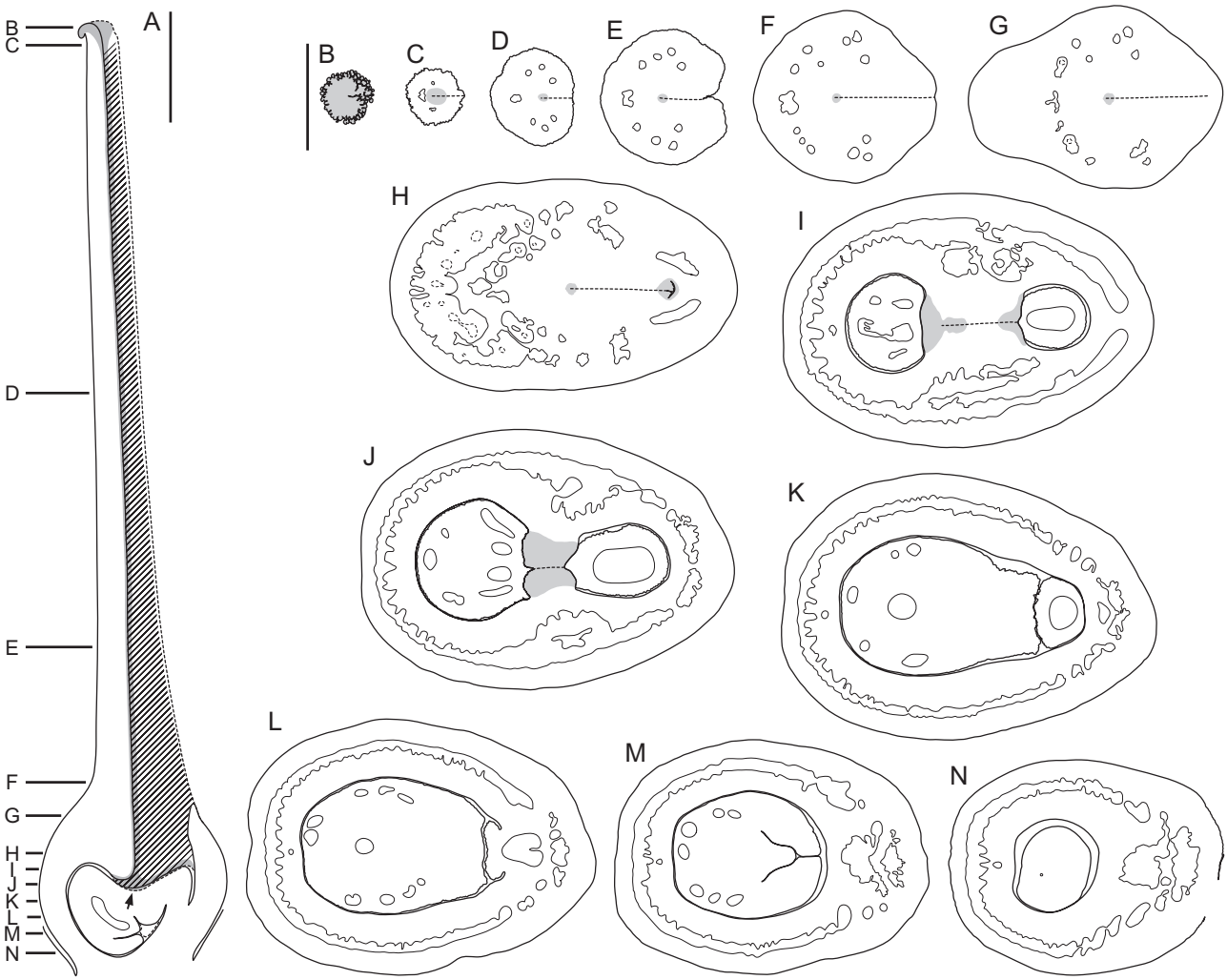


Figure 31. *Anacardium occidentale* (Anacardioideae, Anacardiaceae). Anthetic gynoecium. A, schematic median longitudinal section. B–N, transverse section series. B–F, carpel plicate zone. B, stigma. C–F, style. G–N, carpel ascidiate zone. G–H, above locule. G, carpel cross-zone (transition from plicate to ascidiate zone). I–N, locule, with a single median, basal, anatropous, syntropous, unitegmic ovule. I–J, zone of *ponticulus* [arrow in (A)]. Scale bars, 1 mm (A); 500 μm (B–N).

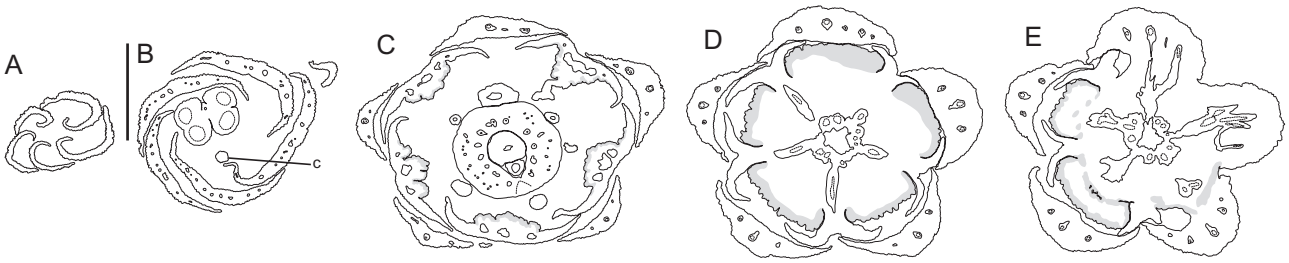


Figure 32. *Mangifera indica* (Anacardiaceae, Anacardioideae). Late female flower bud, transverse section series. A, distal zone, petals contort. B, fertile stamen and carpel (c) antesepalous. C, petal bases with ventral nectariferous ridges, stamens antesepalous, locule with a single ovule. D, floral base, sepals partly imbricate, petal narrow bases with open aestivation, antesepalous extrastaminal nectary lobes. E, sepals uniting with floral base. Scale bar, 1 mm.

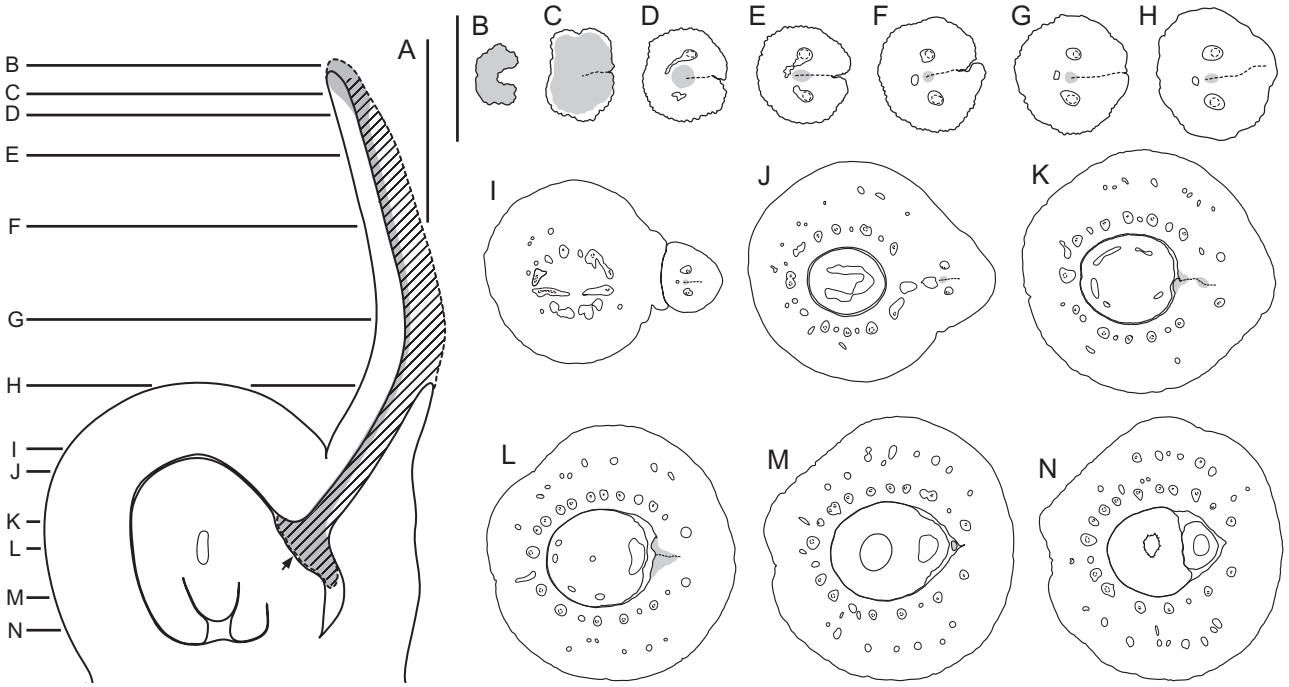


Figure 33. *Mangifera indica* (Anacardiaceae, Anacardioideae). Anthetic gynoecium. A, schematic median longitudinal section. B–M, transverse section series. B–G, carpel plicate zone. B–C, stigma. D–H, style. H–N, carpel ascidiate zone. H, carpel cross-zone (transition from plicate to ascidiate zone). I, bulged up ovary wall, style base. J–N, locule, with a single median, basal, anatropous, syntropous, unitegmic ovule. K–L, zone of *ponticulus* [arrow in (A)]. Scale bars, 500 μm.

The PTTTs of the free carpel tips converge toward the centre of the stigmatic head but a distinct compitum cannot be recognized (Fig. 6A–C). Instead, each PTTT is rapidly restricted to the inner angle of the ventral slit of each carpel and extends separately into the symplicate region, apparently without forming a compitum (Fig. 6A–G). Above the ovary, the carpel flanks are not fused in the inner angle of the ventral slit and form a hollow canal down to the locule (Fig. 6G, H). It remains unclear whether the canal is filled with secretion. In the ovary, the PTTTs follow the ventral angle of each locule down to the placentae (Fig. 6G–J).

Each carpel has a locule with two collateral ovules (Fig. 6H–K). Ovules are crassinucellar, bitegmic, slightly campylotropous, antitropous, with a short funicle inserted ventrally at mid-length of the locule (Fig. 6A). The integuments are sometimes difficult to distinguish from each other. The outer integument is two cell layers and the inner three cell layers thick, but still the outer integument appears thicker than the inner. The inner integument forms a short micro-

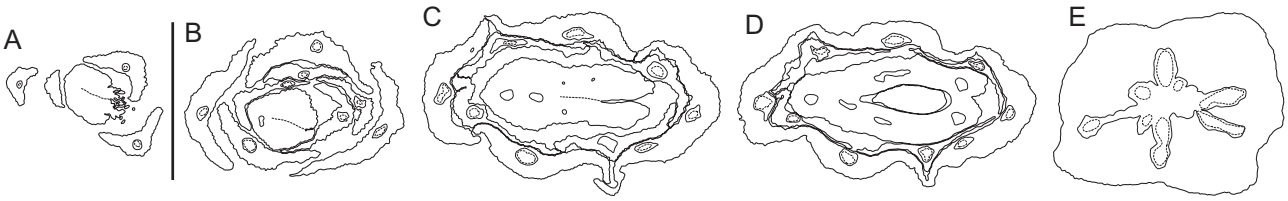


Figure 34. *Blepharocarya involucrigera* (Anacardiaceae, Anacardioideae). Late female flower bud, transverse section series. A, distal zone, sepals, carpel tip with stigma. B, sepals imbricate, petals imbricate and displaced, carpel antesepalous. C, sepals and petals imbricate–valvate, carpel with two conspicuous ventral crests. D, synsepalous zone, petal aestivation open at the base, carpel ascidiate zone, with a single ovule. E, floral base. Scale bar, 250 μm.

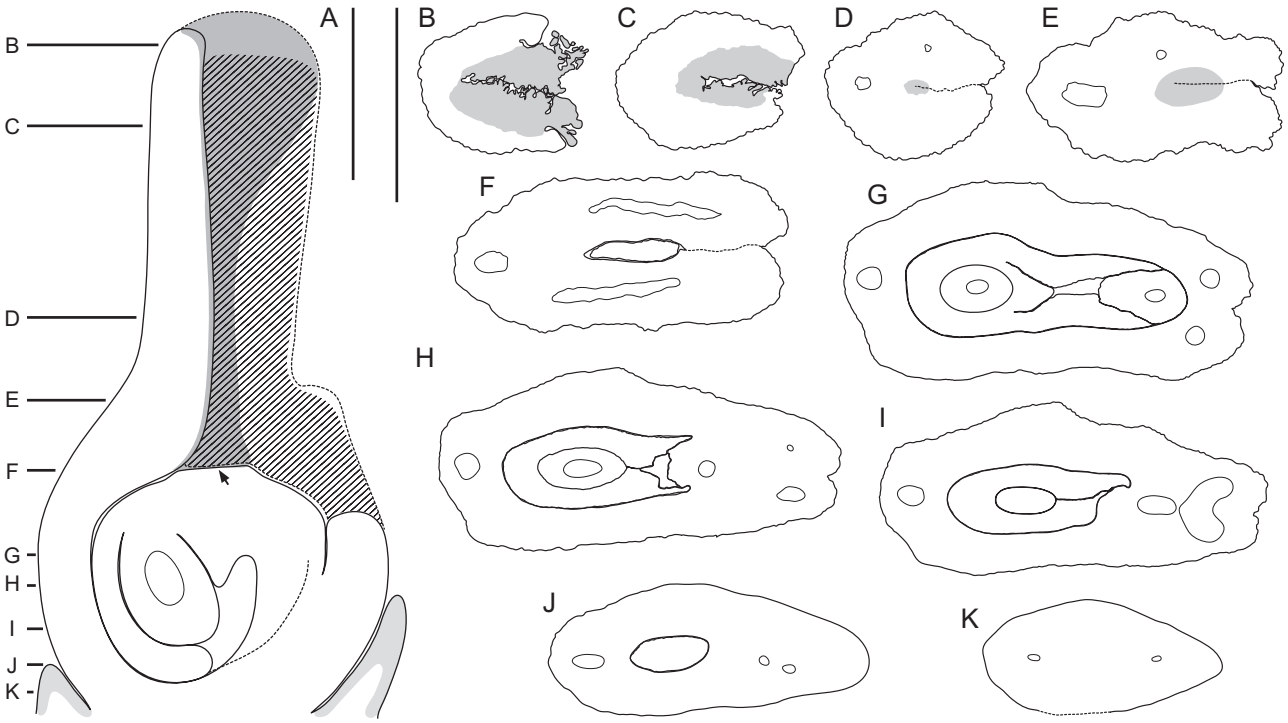


Figure 35. *Blepharocarya involucrigera* (Anacardiaceae, Anacardioideae). Anthetic gynoecium. A, schematic median longitudinal section. B–K, transverse section series. B–F, carpel plicate zone. B, stigma. C–E, style. F–K, ovary. G–J, carpel ascidiate zone. F–J, locule, with a single median, anatropous, syntropous, unitegmic ovule. F, zone of *ponticulus* [arrow in (A)]. K, below locule. Scale bars, 250 μm.

pyle and is surrounded by the shorter and irregularly lobed outer integument (Fig. 6H). The tips of the collateral ovules extend into the base of the stylar canal and the micropyles are contiguous and are in close contact with the PTTT. In the male flowers (*P. obtusifolium*), the gynoecium is sterile and reduced, but in some locules one or two reduced bitegmic ovules are present. If a single ovule is present, it appears to have a median position (Fig. 5D).

Anatomy (P. morii): Vascular bundles have a more or less developed resin canal on the dorsal side of the xylem, except for the ovule bundle (Figs 5, 6). Sepal bases have a median and two lateral main vascular bundles. In the synsepalous region, the lateral bundles form synlaterals, which extend into the floral base (Fig. 5B–E). Petals have a single median vascular bundle at the base. Further up, the median bundle branches and forms a first pair of lateral, smaller vascular bundles (Fig. 5A–E). Each lateral bundle also branches and forms an additional, smaller lateral bundle. By repetition of this process, a petal can have up to nine bundles, which decrease in size toward the margins (Fig. 5A–D). Stamens have a single vascular

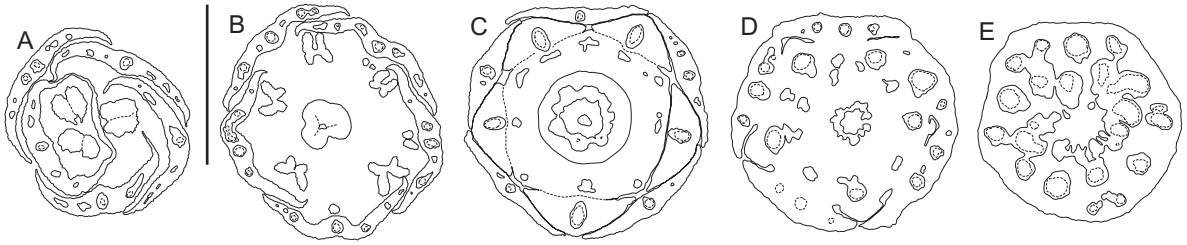


Figure 36. *Schinus molle* (Anacardiaceae, Anacardioideae). Late female flower bud, transverse section series. A, distal zone, petals cochlear, carpel tips. B, antesepalous stamens and two antepetalous stamen tips, gynoecium symplicate zone. C, sepals more or less imbricate, petal aestivation open at the base, ovary locule. D, floral base, sepal flanks still free from floral base. E, floral base. Scale bar, 1 mm.

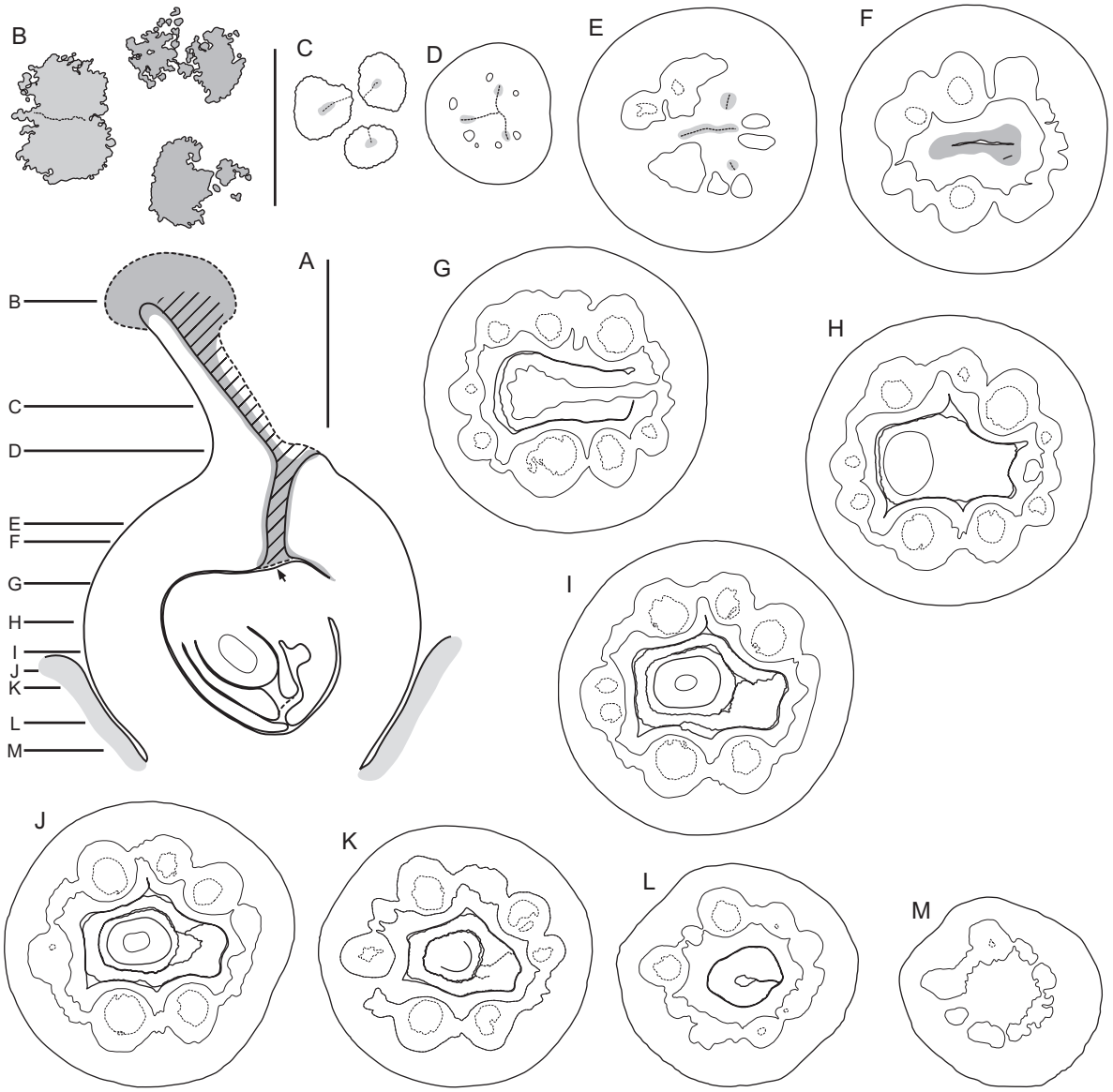


Figure 37. *Schinus molle* (Anacardiaceae, Anacardioideae). Anthetic gynoecium. A, schematic median longitudinal section. B–M, transverse section series. B–C, apocarpous zone. B, stigmas. C, carpels plicate. D–M, ovary. D–F, above locule. D, symplicate zone. F, compitum, zone of *ponticulus* [arrow in (A)]. G–L, locule, with a single median, apical, anatropous, syntropous, bitegmic ovule. M, below locule. Scale bars, 500 μm.

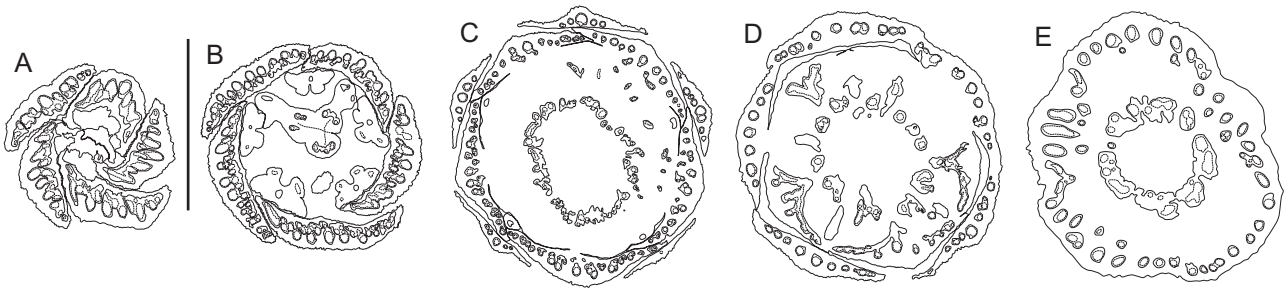


Figure 38. *Semecarpus riparia* (Anacardiaceae, Anacardioideae). Late female flower bud, transverse section series. A, distal zone, petals cochlear with petal tips inflexed. B, stamens antesepalous, carpel tips and gynoecium symplicate zone. C–D, below ovary. C, sepals and petal margins still free. D, synsepalous zone, sepal flanks still free from floral base. E, floral base. Scale bar, 2 mm.

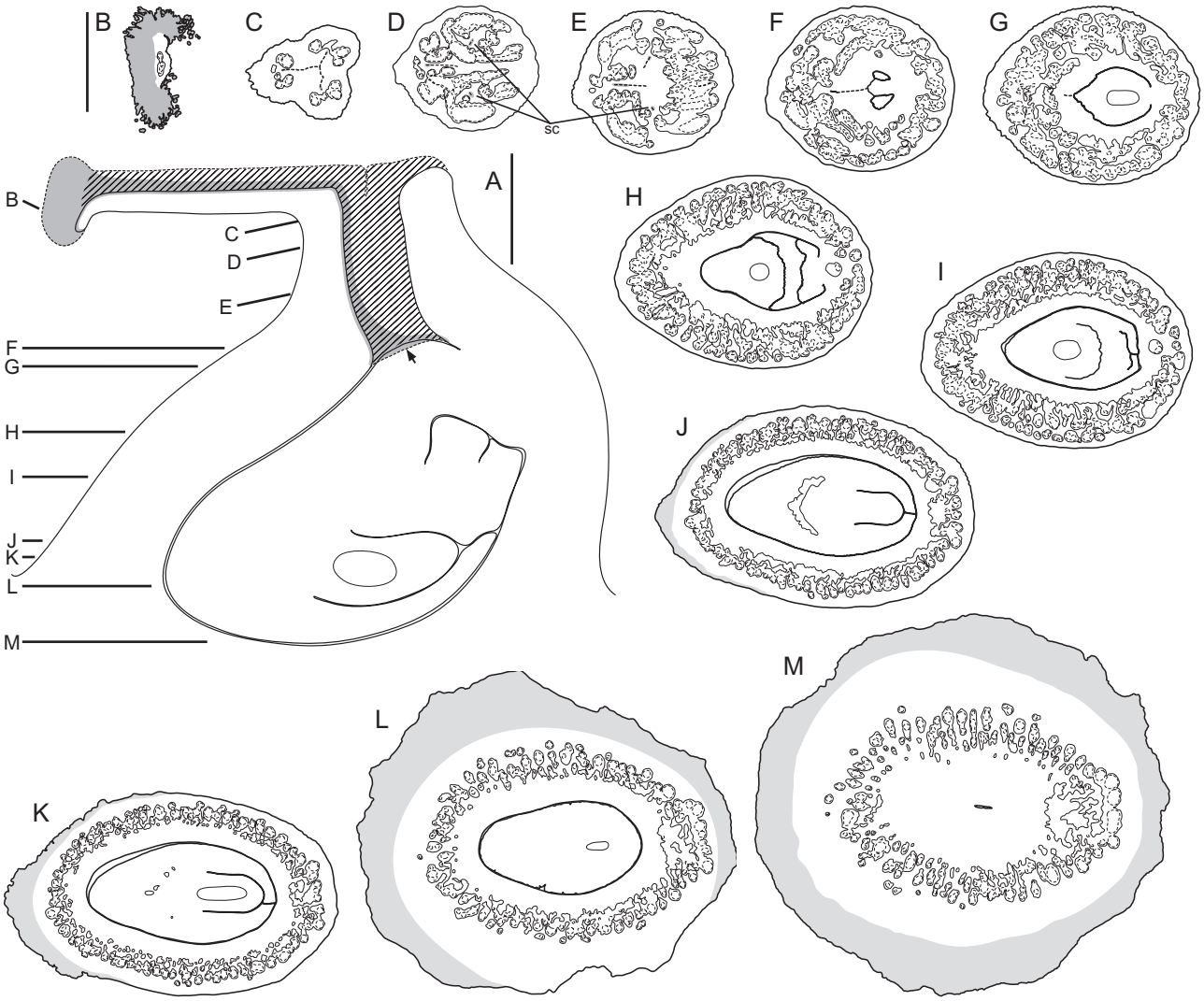


Figure 39. *Semecarpus riparia* (Anacardiaceae, Anacardioideae). Anthetic gynoecium. A, schematic median longitudinal section. B–M, transverse section series. B, stigma. C, symplicate zone. D–M, ovary. D–E, synascidiate zone, traces of inner morphological surfaces of the two sterile carpels still visible (sc). F, zone of *ponticulus* [arrow in (A)]. G–L, locule, with a single median, anatropous, syntropous, bitegmic ovule. M, below locule. Scale bars, 500 μm (A); 1 mm (B–N).

bundle (Fig. 5). In the carpels, a pair of lateral bundles is present in the stigma (Fig. 6C, D). Below the stigmatic head, a median dorsal vascular bundle differentiates but its resin canal only appears towards the base of the style (Fig. 6E, F). Above the ovary, the median dorsal vascular bundle splits into a various number of smaller branches, forming a band of poorly differentiated vascular tissue and resin canals, which extends downwards in the ovary wall and ends in the floral base (Fig. 6G–L). Above the locules, the lateral bundles form synlateral complexes, which are unusual in that they have dorsal xylem and a very large ventral resin canal (Fig. 6H). The synlaterals converge toward the centre of the ovary and form a central vascular complex below the level of the placentae, which for each locule gives off a median ventral vascular bundle splitting into two ovule bundles (Fig. 6I, J). Between the locules, two to three additional resin canals appear in the ovary septa (Fig. 6I–K). Downwards, in the floral base, the petal traces merge with the synlaterals of the sepals of the same radius (Fig. 5E).

Histology (P. morii): Stomata are present on the dorsal side of sepals and petals and on the upper half of the gynoecium, except for the stigmas. The stomata may be slightly raised on the petals. Lignified hairs pointing upwards are found on the floral base, the dorsal side of sepals and petals and on the ovary and style. They are probably unicellular but have a more or less developed branch that points in the opposite direction of the main branch (asymmetric T-shaped hairs). The surface of the nectary disc is slightly papillate and contains nectar pores. A more or less developed striate cuticular ornamentation is present on the floral organs, except for the floral base and the nectary disc. Special mucilage cells are present in the sepal mesophyll (*P. obtusifolium*) or petal mesophyll near the median vascular bundle (*P. morii*) and in the floral base.

Bursera sp. (Burseraceae)
(Figs 7, 40J, K, 44D, 45G)

Morphology: The flowers are morphologically bisexual, trimerous isomerous and obdiplostemonous (Figs 7G′–M′, 40J, K). A floral cup is formed below the petals and stamens (Figs 7H′–L′, 40J).

At anthesis, the acuminate sepals are erect (Fig. 40K). Their bases take part in the floral cup only with their median parts and their margins remain free (Figs 7K′, 40J). The petals also have an open aestivation (Fig. 7G′, H′). They are acute and straight, except for the tips, which are bent inwards (Fig. 40J). Their margins are curved inwards around the antepetalous stamens, whereas the anthers of the antesepalous stamens are exposed between them (Fig. 40J, K). The reproductive organs are shorter than the petals and remain partly hidden by the corolla and floral cup (Fig. 40J, K).

The stamens have a broad flattened filament base, which narrows towards the constricted tip, and a sagittate anther (Figs 7G′, H′, 44D). The anthers are basally dorsifixed and the attachment zone is almost hidden in a pseudopit (Fig. 44D). They may be versatile. They have a thin and narrow connective and a dorsal and a ventral median longitudinal furrow (Fig. 44D). Their dorsal side is broader than the ventral side and the anthers are slightly introrse. The dehiscence lines extend from the tip of the thecae down to their base. A lobed intrastaminal nectary disc is present on the floral cup (Fig. 7G′–L′).

The syncarpous gynoecium is polysymmetric, with as many symmetry planes as the polysymmetric flower (Fig. 7G′–M′). It has a superior ovary and a long style ending in three short stigmatic branches (stigmatic head) (Figs 7A, 40G). Between the carpels, longitudinal furrows extend downwards from the stigmatic head; they end in the middle of the style and, instead, slightly prominent ridges run along the ovary base (Fig. 7C–E, L). The gynoecium is of angiospermy type 4 (Fig. 7). It is synascidiate almost up to mid-length of the ovary and symplicate up to mid-length of the style (Fig. 7A, E–L). Distally, it is apocarpous but the carpels are postgenitally united up to the stigmas (Fig. 7A, C, D). Only the reflexed tips of the carpels are free (Fig. 7A, B). At anthesis, the unicellular and short uniseriate multicellular papillae of the stigmas are covered with secretion (Fig. 7B). In the stigmas, the ventral receptive sides of the carpels form a compitum, which extends downwards into the symplicate zone and splits into three separate PTTTs above the ovary (Fig. 7A–F). Each PTTT reaches the base of the stylar canal and follows the inner angle of the carpels down to the placentae (Fig. 7A, G–J). In our material, the gynoecium of some flowers is not fully developed and the flowers are thus functionally male.

In fully developed gynoecia, each carpel has two collateral ovules per locule (Fig. 7I–K). Ovules are crassinucellar, bitegmic, slightly campylotropous and antitropous, with a very short funicle inserted ventrally in the lower half of the locule (Fig. 7A, I–K). The integuments are sometimes difficult to distinguish. Both integuments are three cell layers thick but the outer integument appears slightly thicker than the inner one on the convex side.The inner integument is longer than the outer one and forms a long S-shaped micropyle (Fig. 7A). The tips of the collateral ovules extend together into the base of the

stylar canal and the contiguous micropyles are in close contact with the PTTT (Fig. 7A).

Anatomy: Vascular bundles have a more or less developed resin canal on the dorsal side of the xylem, except for the ovule bundle (Fig. 7C–I, G′–M′). Sepals have a median vascular bundle, which extends along their entire length, and two smaller lateral ones are often only present at the base. The lateral bundles extend in the floral cup and downwards in the floral base (Fig. 7G′–M′). Petals have a median vascular bundle extending along their entire length and associated at the base with one to two smaller lateral bundles, which extend downwards into the floral cup as two or three traces (Fig. 7G′–M′). Stamens have a single vascular bundle with the resin canal distinctive only in the anther (Fig. 44). In the carpels, a median dorsal vascular bundle is present below the stigmatic region (Fig. 7C–E). Further down, the dorsal bundle splits into two branches (Fig. 7F). The inner portions of those bundles form synlaterals, whereas the peripheral portions form a dorsal arc of bundles (Fig. 7G–J). The synlaterals are unusual in that they have dorsal xylem and a ventral phloem. They extend downwards between the locules and form a central vascular complex in the lower half of the ovary (Fig. 7K, L). The dorsal vasculature forms a band extending downwards in the ovary wall (Fig. 7I–L). Below the level of the placentae, the central vascular complex gives off the ovule bundles (Fig. 7K). In the floral base, the antepetalous stamen traces merge with the petal median (and lateral when present) traces, whereas the three traces of each sepal do not form synlaterals and are the last to merge with the central vasculature (Fig. 7M′).

Histology: Stomata are present on the dorsal side of the sepals and petals. Glandular hairs with multicellular head and uniseriate stalk are sparsely present on the floral cup and sepal margins. The nectary disc has a papillate surface and contains nectar pores. Striate cuticular epidermal ornamentation is more or less conspicuous on the floral organs, except for the gynoecium.

Commiphora caudata (Burseraceae)
(Figs 8, 9, 40L–O, 43C, D, C′, D′, 44E, 45H–J)

Morphology: The flowers are morphologically bisexual and diplostemonous. They have a tetramerous perianth and androecium and a dimerous gynoecium with antepetalous carpels (Figs 8, 40L–O). The flowers are slightly perigynous.

The sepals are congenitally united at the base (Fig. 8B–E). Their tips have an irregularly valvate or imbricate aestivation in early developmental stages (Fig. 8A). Petal tips are valvate and bent inwards, but petal aestivation is open at the base (Figs 8B–D, 40L, N). There is a long intermediate imbricate (sometimes contort) zone (Fig. 8B, C). The corolla becomes longer than the calyx in older buds and protects the reproductive organs up to anthesis (Fig. 40L, N). Postgenital cohesion between the margins of the sepals and petals is formed by interdentation of the papillate epidermis and cuticular ornamentation. Postgenital coherence between the petal margins is only observed for the parts exposed out of the calyx tube. At anthesis, the expanded floral base forms a short floral cup around the ovary base (Fig. 40M, O). Above the floral cup the sepals form a tube and have acute erect free tips (Fig. 8C, D). The acuminate petals are reflexed at mid-length, except for their tips, which retain the inward bend that they had in bud. The shorter reproductive organs remain partly hidden by the calyx tube and corolla (Fig. 40M, O).

The antepetalous stamens are almost twofold shorter and slightly smaller than the antesepalous ones at all stages of development and their anthers are apiculate (Figs 40N, 43C, D). The stamens have a flattened filament base, which becomes rounder and narrows towards the non-constricted tip, and a sagittate anther (Fig. 43C, D). The anthers are dorsifixed in the lower half with a broad and thick connective and only a ventral longitudinal furrow (Figs 43C, D, 44E). The dorsal side of the thecae is longer and broader than the ventral side and the anthers are introrse (Fig. 44E). The dehiscence lines extend from the tips of the thecae almost down to the base (Fig. 43C′, D′). In our material, either male or female organs are sterile and the flowers are thus functionally unisexual. Within the floral cup and calyx tube, the instrastaminal nectary disc is wider in functionally male flowers than in female flowers. The disc has four deep furrows in the petal radii and appears as four antesepalous, slightly bilobed parts. In the centre of the male flower, there is a short aborted gynoecium. In female flowers, the gynoecium prevents the expansion of the nectary disc toward the floral centre and the four furrows are lacking.

The syncarpous gynoecium has a slightly inferior ovary, lacks a distinct style and ends in a bilobed, concave receptive surface (stigmatic head) (Fig. 45H–J). Between the carpels, longitudinal furrows extend from the stigma down to the lower half of the gynoecium. The gynoecium is of angiospermy type 4 (Fig. 9). It is synascidiate up to mid-length of the ovary (Fig. 9A, K, L) and symplicate up to the base of the stigmatic head (Fig. 9A, C–J). Apically, the gynoecium is apocarpous but the plicate stigma bases are postgenitally united (Fig. 9A–C). The stigmas are slightly reflexed (Fig. 9A, B). They have unicellular or

uniseriate 2-3-cellular papillae covered with secretion at anthesis (Fig. 45I). The PTTTs converge toward the centre of the stigmatic head and form a compitum (Fig. 9A–C). The compitum ends in the upper part of the symplicate zone (Fig. 9A, D). Each PTTT follows separately the inner angle of the ventral slit of a carpel and extends downwards into the base of the stylar canal (Fig. 9A, D–J). Lower down, it follows the inner angle of the locule and extends towards the placentae (Fig. 9A, J, K).

Each carpel has a locule with two collateral ovules (Fig. 9H–K). Ovules are crassinucellar and antitropous, with a very short funicle inserted at mid-length of the locule (Fig. 9A). The ovules appear to be unitegmic on the convex side (Fig. 9A, I). The integument is 4–5 cell layers thick. However, on the concave side there is an additional, irregularly lobed outer envelope, which is five to six cell layers thick. It is unclear whether it corresponds to an outer integument (Fig. 9A, I). The longer 'inner' integument forms a slit-shaped micropyle (Fig. 9A). In addition, the collateral ovules are interlocked by lateral projections (or lobes) of their 'outer' integuments. Their tips extend together into the base of the stylar canal (Fig. 9A, G). Their contiguous micropyles face the dorsal region of the locule ceiling and are in close contact with the PTTT (Fig. 9A).

Anatomy: Vascular bundles have a more or less developed resin canal on the dorsal side of the xylem, except for the ovule bundle (Figs 8, 9). Sepals have a median bundle and two main lateral bundles, which extend from their tips down into the floral base (Fig. 8). The free parts of the sepals sometimes have additional, smaller lateral bundles at the base, either between the median bundle and one of the main lateral bundles or towards the periphery (Fig. 8B). All these bundles extend downwards into the synsepalous zone (Fig. 8C–E). Each sepal can have up to seven bundles. The small bundles merge lower down with one of the three main bundles to form three traces and, in the floral base, the main lateral bundles form synlaterals (Fig. 8). Petals have a single vascular bundle at the base, which gives off two main lateral bundles and each branches centrifugally and forms an additional, smaller lateral bundle (Fig. 8B–D). By repetition of this process, a petal can have up to 11 bundles. Stamens have a single vascular bundle with a resin canal only distinctive in filaments of functionally female flowers and less so in functionally male flowers. In the distal part of the anthers, the vascular bundle splits into two branches (Fig. 44E). In the carpels, a median vascular bundle and two slightly shorter lateral bundles are present in the stigmatic region (Fig. 9C, D). Toward the base of the style, the number of bundles increases rapidly (Fig. 9E, F). Some lateral branches converge to form synlateral bundles (Fig. 9E, F), whereas, at the periphery of the locules, the remaining branches form a distinct and discontinuous ring of poorly differentiated vascular tissue with some scarce resin canals (Fig. 9G–M). In the symplicate region of the ovary, the synlaterals extend downwards on each side of the ventral slit and their resin canal is not distinct for some distance (Fig. 9G–K). Below the level of the placentae, the synlateral bundles split into two branches, which serve the adjacent ovules (Fig. 9L, M). The ovule bundle bifurcates in the chalaza but does not reach the integument(s) (Fig. 9K). In the synascidiate ovary base, the synlaterals merge into a central vascular complex, which extends into the floral cup. The petal traces merge with the sepal synlaterals on the same radius in the floral base.

Histology: Stomata are present on the floral cup, on the dorsal side of the sepals and petals, sparsely on the anther tips and on the upper half of the gynoecium, except for the stigmas. The surface of the nectary is smooth and contains nectar pores. Striate cuticular ornamentation is more or less conspicuous on the flower, except for the floral cup and the gynoecium. Special mucilage cells are present in subepidermal and deeper cell-layers of the exposed parts of the perianth, the floral cup and floral base (in the petals also epidermal).

Canarium caudatum (Burseraceae)
(Figs 10, 11, 40P, Q, 44F, 45K, L, 48C, D)

Morphology: The flowers are morphologically bisexual, trimerous, isomerous and obdiplostemonous (Figs 10, 40Q). They have a thick subglobose floral cup (Figs 10D, E, 40P).

The sepals are congenitally united for most of their length (Figs 10, 40P). Their tips form three obtuse and very short lobes and have an open aestivation, but are contiguous in very early stages (Fig. 40Q). Petal aestivation is valvate with the united petal tips bent inwards (Fig. 10B, C), but shortly open at the base and with an intermediate imbricate zone. The corolla becomes longer than the calyx late in development and protects the reproductive organs before anthesis (Fig. 40P). Postgenital cohesion between the valvate margins of the petals is formed by interdentation of papillate epidermis and striate cuticular ornamentation. At anthesis, the expanded floral cup and united sepal bases form a narrow circular aperture surrounded by the sepal tips. The petals are stiff and erect, except for their tips, which retain the inward bend that they had in bud (Fig. 40Q). The reproductive organs are shorter than the petals and remain partly hidden by the corolla and the floral cup

(Fig. 40Q). The stamen bases are united and form a lobed ring around the ovary before they merge with the floral cup. The antepetalous stamens are shorter and slightly smaller than the antesepalous ones at all stages of development (Fig. 45K).

All stamens have a broad flattened filament base, which narrows slightly toward the non-constricted tip, and an apiculate and slightly sagittate anther (Fig. 44F). The anthers are basally dorsifixed and have a broad and thick connective (Fig. 44F). The dorsal side of the thecae is much larger and slightly longer than the ventral side and the anthers are introrse (Fig. 44F). The dehiscence lines extend from below the tip of the thecae down to their base (Fig. 44F). In our material, the anthetic anthers are devoid of pollen and the flowers are thus functionally female. A distinct intrastaminal nectary disc is lacking but the lobes of the stamen ring are nectariferous and alternate with the filaments. The lobes are asymmetrical and more developed adjacent to the antesepalous stamens.

The syncarpous gynoecium is polysymmetric, with as many symmetry planes as the polysymmetric flower (Figs 10D, 11, 40Q). It has a semi-inferior ovary, lacks a distinct style and ends in a trimerous, subglobose receptive part (stigmatic head) (Fig. 45K, L). The gynoecium is of angiospermy type 3 or 4 (Fig. 11). It is almost completely synascidiate in the ovary (Fig. 11A, J–N) and symplicate up to the base of the stigmatic head (Fig. 11A, C–I). Apically, the gynoecium is apocarpous but the apparently unifacial stigmas are postgenitally connected by their uniseriate multicellular papillae (Fig. 11A–C). At anthesis, the stigmas are covered with secretion (Fig. 45L). The PTTTs of the free carpel tips converge toward the centre of the stigmatic head and form a compitum, which extends shortly into the symplicate zone (Fig. 11A–D). Lower down, each PTTT becomes more restricted to the inner angle of the ventral slit of a carpel, in which the carpel flanks are sometimes not fused and may form a hollow canal (Fig. 11A, E–H). It is unclear whether it is filled with secretion. Just above the synascidiate zone, the PTTTs appear to form another compitum (Fig. 11A, I), before they split again and separately follow the ventral angle of each locule, down to the placentae (Fig. 11A, J–L).

Each carpel has a locule with two collateral ovules (Figs 11K–M, 48C). Ovules are crassinucellar, bitegmic, campylotropous and antitropous, with a very short funicle inserted at mid-length of the locule (Fig. 11A). Both integuments are three cell layers thick, but the outer integument appears slightly thicker than the inner one on the convex side. The slit-shaped micropyle is formed by the inner integument, which is surrounded by the shorter and irregularly lobed outer integument (Fig. 48C, D). The tips of the collateral ovules extend together into the base of the stylar canal and the contiguous micropyles face the dorsal region of the locule ceiling and are in close contact with the PTTT (Fig. 11A).

Anatomy: Vascular bundles have a more or less developed resin canal on the dorsal side of the xylem, except for the ovule bundle (Figs 10, 11). The sepals have a median vascular bundle and, at the base, a more or less developed pair of lateral bundles (Fig. 10A). Further up, the lateral bundles either merge with the median dorsal one or end individually in the very short sepal tips (Fig. 10A). Lower down in the synsepalous region, each lateral bundle forms one or more additional, smaller lateral bundles and a sepal can have up to nine vascular bundles (Fig. 10B, C). The median vascular trace extends downwards in the floral cup while the lateral ones tend to merge into synlaterals (Fig. 10D, E). Each petal has a collaterally double median vascular trace in the floral cup, which merges lower down with the synlateral traces of the sepals (Fig. 10D, E). A main pair of laterals merges with the median bundle below the petal insertion level. Each side of a petal can have up to five additional smaller, lateral vascular bundles (Fig. 10B, C). Stamens have a single vascular bundle, from which two laterals branch more or less at the same level in the upper half of the anther. Each branch ends close to a ventral pollen sac (Fig. 44F). In the carpels, only a median vascular bundle is present in the stigmas (Fig. 11C–E). Downwards, the number of vascular bundles of various size and state of differentiation increases and they form a dense network around the locules (Fig. 11G–N). A regular pattern is difficult to recognize. Synlateral bundles are regularly formed from branches of the vascular network above the ovary (Fig. 11H). They extend downards into the ovary septa and converge toward the ovary centre (Fig. 11I–K). Below the level of the placentae, the synlateral bundles unite and form a central vascular complex (without a resin canal), which extends downwards into the floral cup (Fig. 11M, N). This central complex gives off a pair of ovule bundles for each carpel. Each ovule bundle extends shortly in the outer integument (Fig. 11L).

Histology: Stomata are present on the floral cup and rarely on the dorsal side of the anthers. Bicellular lignified hairs pointing upwards are present on the floral cup, the dorsal sepal surface and margins, the petals, the dorsal anther midline and the lateral parts of the thecae. The surface of the nectary is not papillate and it contains nectar pores. More or less developed striate cuticular ornamentation is present, except for the floral cup and the nectary. Special

mucilage cells are present in the distal petal regions, which are exposed out of the floral cup, in the centre of the floral base and in the pedicel.

Santiria cf. *apiculata* (Burseraceae) (Figs 12, 13, 40R–T, 44G, 45M, N)

Morphology: The flowers are morphologically bisexual, trimerous, isomerous and obdiplostemonous (Figs 12, 40T). They have a thick floral cup (Figs 12E, 40S).

The sepals are congenitally united at the base (Fig. 40S). Their tips have an open aestivation and form three acute lobes (Figs 12A–C, 40S). Petal aestivation is valvate, with the united petal tips bent inwards (Figs 12A, B, 40R). At the base it is broadly open (Figs 12D, 40R). There is a slightly imbricate intermediate zone. The corolla becomes longer than the calyx early in development and protects the reproductive organs in bud. Postgenital cohesion between the petal margins is by interdentation of the papillate epidermis and striate cuticular ornamentation (Fig. 40R). Longer uniseriate bi- to tricellular papillae are sparsely present on the inner edges of the petal margins. At anthesis, the floral cup and united sepal bases form a broad circular aperture surrounded by the three stiff free parts of the sepals. The petals are acuminate and erect, except for their tips, which retain the inward bend that they had in bud (Fig. 40S, T). The reproductive organs are shorter than the petals and remain partly hidden by the corolla (Fig. 40S, T).

The stamen bases are united and form a short ring surrounding the upper half of the ovary (Fig. 45M) and merging lower down with the petal bases and the floral cup. The antepetalous stamens are slightly shorter and smaller than the antesepalous ones at all stages of development (Figs 12C, D, 45M). All stamens have a broad flattened filament base, which narrows slightly towards the non-constricted tip, and a slightly sagittate anther (Fig. 44G). The anthers are basally dorsifixed and have a broad and thick connective and a ventral median longitudinal furrow (Fig. 44G). The dorsal side of the thecae is longer and larger than the ventral one and the anthers are introrse (Fig. 44G). The dehiscence lines extend from the tip of the thecae almost down to their base. In our material, the anthers are devoid of pollen and the flowers are thus functionally female. A nectary covers the inner surface of the floral cup and base of staminal ring but does not form a conspicuous disc.

The syncarpous gynoecium is polysymmetric, with as many symmetry planes as the polysymmetric flower (Figs 12D, 40T). It has a globose semi-inferior ovary and a distinct style and ends in a slightly convex, trilobed receptive plate (stigmatic head) (Fig. 45M, N). The gynoecium is of angiospermy type 3 or 4 (Fig. 13). It is synascidiate up to mid-length of the ovary (Fig. 13A, J–L) and symplicate up to the base of the stigmatic head (Fig. 13A, D–I). Apically, the gynoecium is apocarpous, but the stigmas are postgenitally united (Fig. 13A–C). At anthesis, the uniseriate multicellular papillae of the stigmas are covered with secretion (Fig. 45N). The PTTTs converge toward the centre of the stigmatic head and form a compitum, which extends into the symplicate zone (Fig. 13A–E). Lower down, the PTTTs become more restricted to the inner angle of each ventral slit and extend separately down to the locules (Fig. 13A, F–H). Rarely, the flanks of a carpel may not be fused in the inner angle of the ventral slit and may form there a hollow canal. It is unclear whether it is filled with secretion. The PTTT follows the ventral angle of the locule and extends into the ovary down to the placentae (Fig. 13A, I, J).

Each carpel has a locule with two collateral ovules (Fig. 13I–K). Ovules are crassinucellar, seemingly unitegmic, campylotropous and antitropous, with a very short funicle inserted ventrally at mid-length of each locule (Fig. 13A, I, J). The integument is four to five cell layers thick and massive. It forms a long, S-shaped micropyle (Fig. 13A), which is inconspicuous at the surface of the ovule. The tips of the collateral ovules extend together into the base of the stylar canal and the contiguous micropyles face the dorsal region of the locule ceiling and are in close contact with the PTTT (Fig. 13A). At anthesis, only one of the two ovules per locule appears to have a well-developed embryo sac (Fig. 13K).

Anatomy: Vascular bundles have a more or less developed resin canal on the dorsal side of the xylem, except for the ovule bundle (Figs 12, 13). In the synsepalous region, sepals have a median vascular bundle and two smaller lateral ones (Fig. 12E) which form synlateral traces in the floral cup. In their free part, the median vascular bundle gives off a pair of additional, smaller branches and the lateral bundles split into one to two further smaller lateral branches (Fig. 12B–D). Sepals can thus have up to nine vascular bundles. Petals have a median vascular bundle and a pair of smaller lateral bundles. Each lateral may branch and form up to three additional smaller lateral bundles (Fig. 12B–D) and, thus, each petal can have up to nine vascular bundles. Stamens have a single vascular bundle (Fig. 44G). In the carpels, there is no median vascular bundle in the stigmatic region. However, two lateral vascular bundles differentiate below the stigmatic head (Fig. 13D–F), whereas a median dorsal vascular bundle only appears toward the base of the style (Fig. 13G). Lower down, the peripheral portions of the lateral bundles

form a continuous ring of vascular tissue with the median dorsal bundle (Fig. 13H–L), whereas their inner portions form synlateral complexes in the upper end of the ovary (Fig. 13H). The continuous ring of vascular tissue extends downwards in the ovary wall and only the resin canal of the median dorsal vascular bundle is sometimes visible at the level of the locule (Fig. 13I–L). The synlaterals converge toward the centre of the ovary and are unusual in that they have a ventral resin canal and dorsal xylem (Fig. 13H). Each synlateral gives off two branches, which fuse with those of the adjacent synlateral and form a central vascular bundle complex below the level of the placentae (Fig. 13K). Two ovule bundles per locule branch off from this complex and each ovule bundle extends shortly into the integument (Fig. 13K). Below the locules, the ring of vascular tissue no longer appears continuous (Fig. 13L, M), whereas the central vascular traces extend into the floral base. In the floral base, the petal traces fuse with the sepal synlateral traces.

Histology: Stomata are present on the floral cup and on the dorsal side of sepals and petals. Raised stomata on the tip of chimney-like protrusions occur on the floral cup and more sparsely on the dorsal side of the sepal bases and the petal bends. Two- or three-branched unicellular or multicellular hairs are present on the dorsal side of the sepals and floral cup. Unbranched unicellular non-glandular hairs and uniseriate multicellular glandular hairs are present on the dorsal side of the sepals and floral cup. In addition, short (uni- and/or bicellular) lignified hairs develop on the ventral side and margins of the sepals and more sparsely on thecae close to the stomium. The nectary has a smooth surface. It comprises a non-secretory epidermis covered with nectar pores and a cytoplasm-rich mesophyll. Striate cuticular ornamentation is more or less conspicuous on the flower, except for the nectary.

Dracontomelon dao (Anacardiaceae, Spondiadoideae) (Figs 14, 15, 41A–C, 43E, E′, 44H, 46A–C, 48E–G)

Morphology: The flowers are morphologically bisexual, pentamerous, isomerous and obdiplostemonous (Figs 14, 41A, B). The sepals have a quincuncial aestivation and the two outer sepals are larger than the inner ones (Figs 14, 41C). Petal aestivation is cochlear but open at the base (Fig. 14A–C). The petal tips are inflexed and postgenitally connected with the carpel tips in bud (Fig. 41A). The corolla becomes longer than the calyx in late bud and protects the reproductive organs up to anthesis (Fig. 41A). In bud, postgenital cohesion between sepals, petals, sepals and petals, petals and stamens and petal and carpel tips is formed by interdentation of papillate epidermis and striate cuticular ornamentation. However, at anthesis, all these organs are free from each other (Fig. 41B). Sepal aestivation becomes open distally but remains quincuncial at the base (Fig. 41C). Petal aestivation is open almost for the entire length and the margins only overlap distally (Fig. 41B). The corolla is bell-shaped and although stamen filaments are longer than the petals, the narrow corolla aperture prevents the anthers from being exserted and the filaments become irregularly bent. Only the anther tips are exposed together with the receptive stigmas (Fig. 41B).

The antepetalous stamens are slightly shorter and smaller than the antesepalous ones at all stages of development (Fig. 41A). All stamens have a thick and flattened filament base, which narrows slightly towards the constricted tip, and a slightly X-shaped anther (Figs 43E, 44H). The anthers are dorsifixed below mid-length and have a thick and broad connective and a shallow ventral median furrow (Figs 43E, 44H). Their dorsal side is slightly larger than the ventral side and the anthers are slightly introrse, almost latrorse (Fig. 44H). The dehiscence lines extend from the tip of the thecae down to their base (Figs 43E′). In our material, the stamens are devoid of pollen in some buds and these flowers are thus functionally female. A flat intrastaminal nectary disc is present and has erect lobes, which extend between the filaments (Fig. 41A).

The syncarpous gynoecium is polysymmetric, with as many symmetry planes as the polysymmetric flowers. At anthesis, the gynoecium base expands into a stout gynophore. The superior ovary is relatively short and small with regard to the five massive free styles, which are postgenitally united distally at anthesis and form a concave, five-branched plate (stigmatic head) (Fig. 46A, B). Each branch of the stigmatic head corresponds to a slightly reflexed carpel tip and ends in a slit-shaped stigma (Figs 15A, B, 46C). The stigmas do not form a compitum (Figs 15A, B, 46A, B). Between the carpels, deep longitudinal furrows extend along the syncarpous part of the gynoecium down to the gynophore (Fig. 46A). The gynoecium is of angiospermy type 4 (Fig. 15). It is completely synascidiate up to the bases of the styles (Fig. 15A, H–L) and apocarpous further up (Fig. 15A–G). There is no symplicate zone. Below the stigmas, the styles are plicate for some distance (Fig. 15A–E). However, above the ovary, they appear ascidiate (Fig. 15F, G). Although a ventral furrow is visible from the outside, there is no connection to the inside by a ventral slit and there is a median ventral vascular bundle (Fig. 46F, G; see Anatomy). In each stigma, the inner epidermis of the ventral slit differ-

entiates into uniseriate multicellular secretory papillae, which are not exposed (Fig. 46C). The hidden papillae extend into the style down to the postgenitally united region and form a papillate PTTT, in which the ventral slit appears like a zipper (Fig. 46A, B). Lower down, the PTTT gradually becomes restricted to the inner angle of the ventral slit (Fig. 15A–G) and the papillae become shorter and finally reduced to a unicellular papillate epidermis. In the ovary, the PTTTs extend lower down into the base of the stylar canal and toward the placentae (Fig. 15A, H, I).

Each carpel has a single ovule per locule (Fig. 46H, J). Ovules are crassinucellar, bitegmic and syntropous, with a relatively long and bent funicle inserted apically in the inner angle of the locule (Fig. 48E, F). The inner integument is three cell layers thick and the outer integument four (to five) cell layers thick. The outer integument is hood-shaped and not developed on the concave side (Figs 15A, 48F). The inner integument is longer than the outer one but it does not form a micropyle at anthesis and, the tip of the nucellus, faces the placenta (Fig. 48F). In addition, the bend on the dorsal side of the funicle is in close contact with the base of the stylar canal and the PTTT and forms a *ponticulus* (Figs 15A, I, 48F). In one ovary, a second, smaller, antitropous ovule was observed (Fig. 48G).

Anatomy: Vascular bundles have a more or less developed resin canal on the dorsal side of the xylem, except for the stamen and ovule bundle (Figs 14, 15). Sepals can have up to 11 vascular bundles but only the median and two main lateral bundles extend along their entire length (Fig. 14A–D). The additional lateral bundles merge basally on each side of the median vascular bundle with the main laterals, which do not form synlaterals in the floral base (Fig. 14E). Petals have a single median vascular bundle, which extends along their entire length, and four large additional lateral bundles, plus one or two smaller bundles toward the margins (Fig. 14). Stamens have a single vascular bundle (Fig. 44H). In the carpels, small lateral bundles differentiate on each side of the ventral slit in the stigmatic region. Downwards they are quickly followed by a median dorsal bundle, which becomes the largest in the styles (Fig. 15C–E). Towards the ovary, a small median ventral vascular bundle is present (Fig. 15F, G). In the synascidiate region, the median dorsal vascular bundle of each carpel first gives off two small branches. Together with the lateral and ventral bundles of each carpel, they form synlateral bundles, which converge toward the centre of the gynoecium and form a central vascular complex above the locules (Fig. 15H). This complex gives off an ovular bundle for each carpel and extends downwards into the floral base (Fig. 15I–K). Below the locules the dorsal vascular bundle of each carpel merges with the central complex (Fig. 15L). However, the vasculature of the ovary is poorly differentiated at anthesis and scattered undifferentiated strands of vascular tissue are present at the periphery of the locules (Fig. 15I, J).

Histology: Stomata are found on the dorsal side of the sepals. A dense indument of lignified unicellular (or uniseriate bicellular) hairs is present on the floral base and the dorsal side of sepals. Hairs are also present on top of the ovary, the base of the styles, the gynophore and the nectary disc. The nectary contains nectar pores. Non-lignified hairs are present on the dorsal side of the sepals. The surface of the flower is more or less papillate and covered with striate cuticular ornamentation.

Spondias dulcis (Figs 16, 17, 41D, 43F, F′, 44I, 46D–G, 48H, I) and *S. purpurea* (Figs 18, 19, 41E–H, 44J, 46H–I) (Anacardiaceae, Spondiadoideae)

Morphology: The flowers are morphologically bisexual, pentamerous, isomerous and obdiplostemonous (Figs 16, 18, 41D–H). Sepals are free (Fig. 16B–D). They have a quincuncial aestivation in very young buds and the two outer sepals are slightly larger than the inner ones (Fig. 41H). Later, their aestivation becomes open but their margins still shortly overlap at the base. In contrast, petal aestivation is valvate, with the petal tips hooded around the carpel tips (Figs 16A–D, 18A–C, 41E, F). Only at the base is it shortly open (Fig. 16D). The corolla becomes longer than the calyx early in development and protects the reproductive organs up to anthesis (Figs 16, 18, 41E, F). Postgenital coherence between the petal margins in bud is formed by interdentation of their papillate surface and striate cuticular ornamentation. At anthesis, the expanded petals are free, recurved backwards (*S. dulcis*, Fig. 41D) or upright (*S. purpurea*, Fig. 41G), except for their acute tips, which retain the inward bend that they had in bud (Fig. 41G). The reproductive organs are completely exposed (*S. dulcis*, Fig. 41D) or remain partly hidden (*S. purpurea*, Fig. 41G).

The antepetalous stamens are shorter, and narrower (*S. purpurea*, Fig. 41F), than the antesepalous ones at all stages of development. All stamens have a flattened filament base, which becomes rounder and narrows toward the constricted tip, and an X-shaped anther (Figs 43F, 44I, J). The anthers are dorsifixed in the lower half (*S. dulcis*, (Fig. 43F) or at the base

(*S. purpurea*) and they have a relatively broad and thick connective and a shallow dorsal and a ventral (only ventral in *S. purpurea*) longitudinal furrow (Fig. 44I, J). Their dorsal side is broader (and longer in *S. purpurea*) than the ventral side and they are slightly introrse (Fig. 44I, J). The dehiscence lines extend from the tip of the thecae almost down to their base (Fig. 43F′). In our material the anthers are devoid of pollen in *S. dulcis* and *S. purpurea* and the flowers are thus functionally female. A thick lobed intrastaminal nectary disc is present and surrounds the lower half of the ovary (Fig. 41D, F).

The syncarpous gynoecium is polysymmetric, with as many symmetry planes as the polysymmetric flower (Figs 16, 18, 41D, G). It has a superior ovary (Figs 16, 18, 41D, F, G). There are five free styles, which are longer than the ovary, massive and connivent in *S. dulcis* (Fig. 46D, E), and shorter than the ovary and arranged at the periphery of the flat roof of the ovary in *S. purpurea* (Fig. 46H). Between the bases of the style, longitudinal furrows extend shortly downwards and vanish at mid-length (*S. dulcis*) or at the upper end (*S. purpurea*) of the ovary. The gynoecium is of angiospermy type 4 (Figs 17, 19). It is entirely synascidiate up to the base of the free styles (Figs 17A, H–L, 19A, E–L, 41D). There is no symplicate zone (Figs 17A, 18A). The styles are plicate up to the stigma and have a conspicuous ventral longitudinal furrow (Figs 17A–G, 19A–D, 41D). The stigma is covered with uniseriate multicelllular and secretory papillae (Fig. 46F, I). In *S. purpurea*, it appears as if the distalmost part of the ventral slit of each carpel is rolled outwards to expose the stigmatic surface (Fig. 17A–C). In *S. dulcis*, the contiguous stigmas may form an external compitum at anthesis (Figs 17B, 46D, E). The stigmas are covered with uniseriate multicellular papillae (also some unicellular in *S. purpurea*). After anthesis, the expansion of the ovary roof leads to the displacement of the persistent styles toward the periphery of the fruit (Fig. 46G). Below the stigmas, the papillae extend downwards into the styles and form distinct papillate PTTTs. Downwards, each PTTT becomes restricted to the inner angle of the ventral slit of the carpel and is only slightly papillate (Figs 17A–G, 19A–D). In the synascidiate zone, the PTTTs extend separately toward the base of the stylar canals and placentae (Figs 17A, H, I, 19A, E–G). They also form large papillae towards the ceiling of the locule in *S. dulcis* (Fig. 17I, J).

Each carpel has a uniovulate locule (Figs 17I–L, 19G–K). Ovules are crassinucellar, bitegmic and syntropous, with a relatively long (longer in *S. purpurea*) and bent funicle inserted apically in the inner angle of the locule (Figs 17A, 19A). The inner integument is three (four) cell layers thick and the outer three cell layers thick in *S. dulcis*. In *S. purpurea* the inner integument is four (five) cell layers thick and the outer three (four) cell layers thick.The outer integument is hood-shaped and not developed on the concave side. In *S. dulcis* the inner integument is longer than the outer one, but the micropyle is not closed at anthesis and the tip of the nucellus faces the placenta (Figs 17A, 48H), whereas in *S. purpurea*, the inner integument is shorter than the outer one and forms an endostomial slit-shaped micropyle, hidden by the outer integument, which has two large lateral flaps wrapped around the inner parts of the funicle–ovule complex (Fig. 19A). In the region of the bend, the funicle has a dorsal outgrowth, which is in close contact with the papillae in the base of the stylar canal and forms a *ponticulus* (Figs 17A, I, J, 19A, G). In *S. dulcis*, the funicle is postgenitally connected after anthesis with the base of the stylar canal and the micropyle is closed (Fig. 48I). It is formed by the still longer inner integument, which is thickened above the nucellus. In addition the ovule becomes slightly campylotropous and the contact between the two integuments becomes loose. In *S. purpurea* the ovules are aborted after anthesis in our material and the flowers may thus be functionally sterile.

Anatomy: Vascular bundles have a more or less developed resin canal on the dorsal side of the xylem, except for the stamen and ovule bundles (Figs 16–19). In *S. dulcis*, resin canals are present only in the main vascular bundles of the perianth and the dorsal vascular bundle of the carpels [in the latter they are hypertrophic (Fig. 17D–K)]. Sepals have a median vascular bundle at the base and one or two lateral smaller bundles (depending of the sepal position in *S. purpurea*) and they do not form synlaterals (Fig. 18D). Petal bases have a single, median vascular bundle, which further up gives off two smaller lateral bundles (Figs 16C, D, 18C, D). Additional smaller vascular bundles connect with the median and lateral bundles and a petal can have up to seven vascular bundles in *S. dulcis* (Fig. 16A, B) and only up to four to five in *S. purpurea* (Fig. 18A, B). Stamens have a single vascular bundle (Fig. 44I, J). In the carpels, a dorsal vascular bundle differentiates below the stigmas and extends downwards into the floral base (Figs 17D–L, 19B–L). It is followed in the style by two lateral bundles (Figs 17D–H, 19C–F). Branches of the lateral bundles form synlaterals in the upper ovary and converge towards its centre, whereas the peripheral branches extend in the ovary wall between the dorsal bundles of adjacent carpels (Figs 17I–L, 19G–K). The synlaterals form a central vascular complex, which gives off a ventral median vascular bundle for each carpel serving the ovule. The synlaterals extend separately downwards, surrounding isolated xylem

strands, which are present along the entire length of the ovary (Figs 17I–L, 19G–K). In the floral base, the petal traces merge with the sepal synlaterals of the same radius. At anthesis, the vasculature is not well developed in the ovary and largely consists of procambial strands (Fig. 18D).

Histology: In *S. dulcis* stomata are present on the dorsal side of sepals, petals and stamens, at the transition from filament to anther, and in *S. purpurea* they are present only on the dorsal side of the sepals and petals. In *S. dulcis*, the flower is glabrous, whereas in *S. purpurea* the sepals have hairs at the basal dorsal side and their margins are fringed. The surface of the nectary disc is papillate and contains nectar pores. Striate cuticular ornamentation is conspicuous on the flower, especially on the dorsal side and margins of petals, but is lacking on the nectary disc in *S. dulcis*.

Pleiogynium solandri (Anacardiaceae, Spondiadoideae) (Figs 20, 21, 41I–L, 43G, H, G′, H′, 44K, 46J, K, 48J, K)

Morphology: The flowers are morphologically bisexual but functionally unisexual and the functionally male flowers are smaller than the female ones (Figs 20, 41I–L). Male flowers are polysymmetric, pentamerous, isomerous and obdiplostemonous (Figs 20E, 41I). Female flowers vary in carpel number (Figs 21, 41K, L).

The free sepals have a quincuncial aestivation in young buds and the two outer sepals are slightly larger than the inner ones (Fig. 20A–D). Later in development, their aestivation becomes open for their entire length (Figs 20E, 41K). Petal aestivation is cochlear (Fig. 20B). The corolla becomes longer than the calyx in bud and protects the reproductive organs up to anthesis (Fig. 41I). Postgenital cohesion between the margins of the petals in bud is formed by interdentation of the slightly papillate epidermis and striate cuticular ornamentation. At anthesis, the expanded petals are free and recurved. The reproductive organs are entirely exposed (Fig. 41J–L). The petals have conspicuous longitudinal ridges in the lower half of the ventral side (each ridge lies over a vascular bundle and its resin canal is visible as a dark line) (Figs 20B, 41J, L). A median dorsal ridge expands between the sepals.

The antepetalous stamens are shorter than the antesepalous ones at all stages of development and their anthers are apiculate vs. non-apiculate (Figs 41I, J, 43G, H). All stamens have a broad flattened filament base, which further up becomes rounder and narrows towards the constricted tip, and a sagittate anther (Fig. 44K). The anthers are dorsifixed in the lower half (Fig. 43G, H). The connective is intermediate in thickness and the antepetalous anthers have a longitudinal furrow on the ventral side (Fig. 44K). In antesepalous stamens the dorsal parts of the thecae curve backwards and form a pseudopit around the filament tip (Fig. 44K). The dorsal side of the anthers is broader and longer than the ventral side and they are thus introrse (Fig. 44K). The dehiscence lines extend from the tip of the thecae almost down to their base (Fig. 43G′, H′). A thick lobed intrastaminal nectary disc is present and surrounds the base of the superior ovary.

In functionally female flowers the syncarpous gynoecium consists of seven to ten carpels and is polysymmetric (Figs 20B, C, 21B–J, 41K, L). However, the variable number of carpels often leads to a mismatch of the symmetry planes of the gynoecium and the perianth plus staminodes and the female flowers are thus not always strictly polysymmetric (Figs 20B, C, 41K, L). The styles are much shorter than the large ovary (Fig. 21A–C). They are arranged in a ring around the large and slightly convex central region of the ovary (Figs 21B, C, 46J). The gynoecium is of angiospermy type 4 (Fig. 21). It is synascidiate in the ovary (Fig. 21A, C–J), but apocarpous further up (Fig. 21A–C). There is no symplicate zone. The free zone of the carpels is plicate and has a ventral longitudinal furrow, which extends from the stigma (almost) down the synascidiate region (Figs 21A–C, 46K). Sometimes, the distance between the carpels is not equal and neighbouring styles with short distances may be partially congenitally united (Fig. 21D, E). The minute stigmas have uniseriate multicellular secretory papillae, which expand through the distal part of the ventral slit of each carpel (Fig. 46K). When the flowers open, the styles are contiguous and the stigmas may contact each other and thus form a ring-shaped compitum (Fig. 46J). However, the expansion of the ovary roof during anthesis moves the styles toward the periphery of the gynoecium and the stigmas lose contact (Fig. 21B, C). After anthesis, the styles are further displaced toward the periphery of the developing fruit and later abscise (Fig. 41L). Below the short stigmatic region, a PTTT differentiates along the ventral slit in each carpel and downwards it becomes restricted to the inner angle of the ventral slit (Fig. 21A–C). It extends into the base of the stylar canals and the placentae (Fig. 21A–F).

Each carpel has a single ovule (Fig. 21I, J). Ovules are crassinucellar, bitegmic and syntropous, with a long and bent funicle inserted apically in the inner angle of the locule (Fig. 21I, J). The inner integument is three (four) cell layers thick and the outer one four (five) cell layers thick. The inner integument is shorter than the outer one and forms a slit-shaped endostome hidden by the hood-shaped outer integu-

ment, which forms lateral flaps around the inner parts and gives the ovule the appearance of a bat hanging in its cave (Figs 21A, I, J, 48J, K). In the region of the bend, the dorsal side of the funicle is in close contact with the base of the stylar canal where the PTTT ends and forms a *ponticulus* (Figs 21A, I, J, 48J).

Anatomy: Vascular bundles have a more or less developed resin canal and a ventral xylem, except for the ovule bundle (Figs 20, 21). Sepals have a median vascular bundle, which extends along their entire length, and two shorter main lateral vascular bundles (Fig. 20A–D). Further up, the three bundles branch, forming additional, smaller bundles, which are intercalated between the median and the two main lateral bundles or toward the sepal margins (Fig. 20B, C). A sepal can have up to eight vascular bundles. At the sepal base, the two main lateral bundles may not merge with the median bundle (Fig. 20D). They do not form synlaterals (Fig. 20D). Petals have a median and two lateral bundles, which extend along their entire length and they merge in the floral base (Fig. 20B, C). Further up, each lateral bundle branches, forming an additional smaller lateral bundle toward the petal margin and, by repetition of this process, the petals can have up to nine vascular bundles. Stamens have a single vascular bundle, which in the anther comprises a large resin canal (Fig. 44K). In the carpels, the dorsal vasculature is poorly differentiated in the ovary wall (Fig. 21G–J), whereas, below the stigma, a median dorsal vascular bundle is present and branches, forming a lateral smaller bundle on each side of the ventral slit towards the base of the short style (Fig. 21B–D). In the upper end of the synascidiate region, each dorsal vascular bundle forms numerous smaller branches extending sideways as an arc with more or less differentiated resin canals (Fig. 21E, F). Downwards, the arcs almost form a continuous band in the ovary wall. The lateral vascular bundles converge toward the centre of gynoecium (Fig. 21G–J). They form a reticulate vascular network in the ovary roof and form synlaterals between the locules. Neighbouring synlaterals form a median vascular bundle for each carpel, which connects to the placenta and ovule (Fig. 21F) and, downwards, they extend separately in the centre of the ovary (Fig. 21G–J). At the base of the ovary, the synlaterals first unite with each other and merge lower down with the peripheral band of vasculature.

Histology: Stomata are found sparsely on the dorsal side of the sepals and petals and anthers above the attachment zone. Lignified unicellular hairs (or seemingly bicellular) are present on the scarcely fringed sepal margins. The surface of the nectary disc is papillate and contains nectar pores. Striate cuticular ornamentation is more or less conspicuous on the entire flower.

Pseudospondias longifolia (Figs 41N, 43I, I′, 44L) and *P. microcarpa* (Figs 22, 41M) (Anacardiaceae, Spondiadoideae)

Morphology: The flowers are morphologically bisexual, polysymmetric, tetramerous (*P. microcarpa*) or trimerous (*P. longifolia*), isomerous and obdiplostemonous (Figs 22, 41M, N). The sepals are very shortly congenitally united. Sepal aestivation in bud is cochlear but distally appearing as two decussate pairs in *P. microcarpa* (Fig. 22A–D). Petal aestivation is cochlear but shortly open at the base (Fig. 22B–D). The petals become longer than the sepals in bud and protect the inner organs up to anthesis. Postgenital coherence between the overlapping margins of the petals is formed by interdentation of their papillate surface and striate cuticular ornamentation. At anthesis, the expanded petals are free and their margins are slightly curved inwards (Fig. 41M, N). The inner floral organs are largely exposed (Fig. 41M, N).

The antepetalous stamens are slightly shorter than the antesepalous ones at all stages of development (Fig. 41M). All stamens have a broad flattened filament base, which becomes rounder and narrows toward the constricted tip, and a slightly X-shaped anther (Figs 43I, 44L). The anthers are dorsifixed at mid-length of the thecae and have a thin and narrow connective and a dorsal and a deep ventral longitudinal furrow (Figs 43I, 44L). Their dorsal side is larger than the ventral side and they are slightly introrse (Fig. 44L). The dehiscence lines extend from the tip of the thecae down to their base (Fig. 43I′). A thick lobed intrastaminal nectary disc is present and surrounds the base of the superior ovary.

The syncarpous gynoecium is polysymmetric, with as many symmetry planes as the polysymmetric flowers (Fig. 22C, D). The gynoecium is synascidiate in the ovary (Fig. 22D) and apocarpous further up (Fig. 22C). It is unclear whether a symplicate region is present (Fig. 22C). In our material, the ovary locules are reduced and lack an ovule and the flowers are functionally male.

Tapirira guianensis (Anacardiaceae, Spondiadoideae) (Figs 23, 41O, P, 43J, J′, 44M)

Morphology: The flowers are morphologically bisexual, polysymmetric, pentamerous or tetramerous, isomerous and obdiplostemonous (Figs 23, 41O, P). The difference in size of the sepals suggests that they are spirally initiated. They are basally congenitally united

(Fig. 23E). Petal aestivation is cochlear but slightly open at the base (Fig. 23E). The petals become longer than the sepals early in young buds and the corolla protects the inner organs up to anthesis (Fig. 23). Postgenital coherence between the petals is formed by interdentation of their papillate surface and striate cuticular ornamentation. At anthesis, the free parts of the obtuse sepals have an open aestivation. The expanded petals are free and reflexed (Fig. 41O, P). The inner floral organs are entirely exposed (Fig. 41P).

The stamens have a broad and thick filament base, which becomes rounder and narrows toward the constricted tip, and a sagittate anther with a short connective tip (Figs 43J, 44M). The anthers are basally dorsifixed and have a thin and narrow connective and a dorsal and a deep ventral longitudinal furrow (Fig. 44M). They are slightly introrse and the dehiscence lines extend from the tip of the thecae down to their base (Fig. 43J′). A thick lobed intrastaminal nectary disc is present and surrounds the base of the superior ovary (Fig. 23D).

In our material, the gynoecium is reduced and the flowers are functionally male. The (reduced) syncarpous gynoecium is polysymmetric, with as many symmetry planes as the polsymmetric flower, although one carpel is often missing to make the flower isomerous. The ovary has a single locule and axile median, apical (reduced) ovule and appears pseudomonomerous (Fig. 23C, D). Above the ovary, the gynoecium is apocarpous (Fig. 23B).

Buchanania arborescens (Anacardiaceae, Spondiadoideae) (Figs 24, 25, 41Q–S, 44N, 46L–N)

Morphology: The flowers are morphologically bisexual (Figs 24, 41Q–S). Perianth and androecium tend to be isomerous, with (3–) 4–5 (–6) organs per whorl (Fig. 24). When the whole flower is isomerous, it is polysymmetric and obdiplostemonous (Fig. 41R, S). However, there is more often one carpel less and, rarely (when the perianth and androecium are trimerous), one carpel more.

The sepals are basally congenitally united and have an open aestivation (Fig. 24D). Petal aestivation is cochlear (the position of some petal margins may change within a bud) but almost valvate at the base (Fig. 24A–D). The corolla becomes longer than the calyx very early in development and protects the reproductive organs in bud (Fig. 41Q). Postgenital cohesion between the petals is formed by interdentation of their slightly papillate surface and striate cuticular ornamentation. At anthesis, the expanded petals are free and reflexed backwards. The reproductive organs are entirely exposed (Fig. 41Q).

The stamens have a flattened filament, which narrows toward the constricted tip, and a sagittate anther (Figs 24D, 41Q). The anthers are basifixed and may be versatile (Fig. 41S) and the attachment zone is almost hidden in a pseudopit (Figs 41Q, 44N). The connective is intermediate in thickness and there is a deep dorsal and ventral longitudinal furrow (Fig. 44N). The pollen sacs do not extend into the free basal parts of the thecae (Fig. 44N). The anthers are almost latrorse and the dehiscence lines extend from the tip of the thecae down to where the pollen sacs end (Fig. 44N). In our material, most anthers are devoid of pollen and the flowers are functionally female. A thick lobed intrastaminal nectary disc is present and is much thicker toward the centre than at the periphery so that only the connivent styles (more or less reflexed distally) and stigmas are visible of the gynoecium (Fig. 41S).

Although the gynoecium appears polysymmetric, the variable number of carpels often leads to a mismatch of the gynoecium symmetry planes with those of the other parts of the flower (Fig. 24) and the flowers are rarely completely polysymmetric (Fig. 41R, S). In addition, only one carpel is fertile and the gynoecium is thus structurally monosymmetric (Figs 25, 46L, M). The fertile carpel has a superior ovary and a short style lacking a stigma, whereas the sterile carpels lack a locule and ovule and only develop into a long style ending in a receptive stigma (Figs 25A–C, 46L–N). The gynoecium is of angiospermy type 4 (Fig. 25). It is largely apocarpous, (Fig. 25A–I, 46L) but basally syncarpous with an extremely short synascidiate zone (Fig. 25A, J, K). There is no symplicate zone. The free parts of the carpels appear shortly ascidiate basally, especially in the fertile carpel (Fig. 25A, I, J), and are otherwise plicate with a ventral longitudinal furrow covered with secretion at anthesis (Fig. 25A, B–H). The sterile carpels are longer than the fertile one and have well-developed stigmas, whereas the fertile carpel does not have a differentiated stigma (Fig. 46M). The stigmas have uniseriate multicellular secretory papillae (Fig. 26N). Below the stigma of the sterile carpels, the PTTT differentiates along the ventral slit (Fig. 25A). It is slightly papillate and appears like a zipper. Downwards, it becomes more restricted to the inner angle of the ventral slit and ends in the ascidiate base (Fig. 25A–K). In contrast in the fertile carpel, a PTTT is observed only just above the locule and ends at mid-length of the style (Fig. 25A, F).

The fertile carpel has a single ovule, which is crassinucellar, bitegmic, syntropous and hangs from a long funicle inserted basally in the inner angle of the locule (Fig. 25A). The outer integument appears thicker than the inner one although both integuments are three (four) cell layers thick. The inner integu-

ment is longer than the outer one and forms the micropyle, which faces the floor of the locule (Fig. 25A). On the dorsal side of the funicle–ovule complex, there is a dorsal outgrowth in the region of the bend, which projects into the base of the stylar canal and is in close contact with the PTTT. It could be interpreted as a *ponticulus* (Fig. 25A, F). At anthesis, pollen has been only observed on the receptive stigmas of the sterile carpels (Fig. 46L). It is unknown how pollen tubes move from the sterile carpels to the fertile carpel (see Discussion).

Anatomy: Vascular bundles comprise a more or less conspicuous resin canal and a ventral xylem, except for the stamen and ovule bundles (Figs 24, 25). Sepals have a main median vascular bundle and, in the synsepalous region, synlateral bundles are sometimes present (Fig. 24C–E). Petals have a median vascular bundle, which extends along the entire length and branches, forming smaller lateral vascular bundles at different levels (Fig. 24B–D). Stamens have a single vascular bundle (Figs 24B–D, 44N). In the carpels, a dorsal vascular bundle extends along their entire length (Fig. 25B–L). In the sterile carpels, a pair of lateral vascular bundles on each side of the ventral slit extends down to the ovary base (Fig. 25B–K). In the fertile carpel, lateral vascular bundles branch from the median dorsal bundle only in the upper part of the ovary (Fig. 25F). Downwards, they extend toward the ventral side of the carpel and form a network around the locule (Fig. 25G–K). Toward the base of the locule, a median ventral bundle is formed and branches, forming the ovule bundle (Fig. 25I, J). Synlateral bundles are formed in the syncarpous base of the gynoecium (Fig. 25K, L).

Histology: Stomata are observed on the dorsal side of the sepals, on anther tips and more sparsely on carpel tips (fertile and sterile). Lignified unicellular hairs are present on the fringed margins of the sepals and on the carpels. Glandular hairs with uniseriate multicellular stalks and multicellular heads are present only on the gynoecium. Hairs are more abundant on the fertile carpel than on the sterile ones (Fig. 46L). The surface of the nectary disc is papillate and contains nectar pores. Striate cuticular ornamentation is conspicuous on the entire flower, especially on the anthers.

Solenocarpus philippinensis (Anacardiaceae, Spondiadoideae) (Figs 26, 27, 42A, 44O, 46O, P)

Morphology: The flowers are bisexual and diplostemonous (Fig. 26). Perianth and androecium are pentamerous and the gynoecium is monomerous (Fig. 26). The flowers are thus monosymmetric (Figs 26, 42A).

The sepals are basally congenitally united (Fig. 26E). Their triangular free parts are short and have an open aestivation in preanthetic bud (Fig. 26D). Petal aestivation is valvate (Fig. 26A, B), although some petal margins are asymmetrical at the base (Fig. 26C, D). The petal tips are folded inwards around the anther tips (Fig. 26A). The corolla becomes longer than the calyx early in development and protects the reproductive organs up to anthesis (Fig. 26). Postgenital cohesion between the petal margins is formed by interdentation of the papillate epidermis and striate cuticular ornamentation. At anthesis, the expanded acute petals are free and reflexed, except for their margins and tips, which retain the inward inflexion they had in bud (Fig. 42A). The reproductive organs are entirely exposed (Fig. 42A).

All stamens have a large and thick filament base (Fig. 26C), which becomes rounder further up and narrows towards the constricted attachment zone, and a sagittate anther. The anthers are dorsifixed in the lower half of the thecae and may be versatile and caducous. The connective is extremely broad and thick and the dorsal side of the thecae curves backward and almost forms a pseudopit around the attachment zone (Fig. 44O). In our material, in late anthetic flowers all anthers were fallen and in the single bud we could study they were latrorse (slightly introrse), with longitudinal dehiscence lines extending from the tip of the thecae down to their base (Fig. 26A, B). A thick lobed intrastaminal nectary disc surrounds the base of the superior ovary (Fig. 26C).

The single carpel is antepetalous (Fig. 26C). It comprises a globose ovary and a short apical dorsal style, ending in a long flat and oblique stigma (Fig. 46O, P). The carpel is of angiospermy type 4 (Fig. 27A). It is ascidiate almost up to the stigma lower half of the style (Fig. 27A, G–R) and plicate further up (Fig. 27A–F). A ventral longitudinal furrow extends from the base of the stigma down to middle of the style (Figs 27A–G, 46P). The stigma has short unicellular and two- to three-cellular uniseriate papillae, which are densely packed and are covered with secretion at anthesis (Fig. 46P). After anthesis, style and stigma are displaced toward the dorsal side of the carpel. Below the papillae, a PTTT differentiates along the ventral slit (Fig. 27A). In the style, the PTTT becomes more restricted to the inner angle of the ventral slit (Fig. 27F–I) and extends into the ovary down to the base of the stylar canal and the placenta (Fig. 27J–L).

The carpel has a single ovule, which is crassinucellar, perichalazal, bitegmic and syntropous and has a long and bent funicle inserted apically in the inner angle of the locule (Fig. 27A, K–Q). Both integuments

are three (four) cell layers thick, but the outer one appears slightly thicker than the inner. The micropyle is formed by both integuments. (Fig. 27A). The hood-shaped outer integument is longer than the inner on the convex side and has two lateral flaps folded around the inner parts and the funicle base (Fig. 27A, K–Q). The inner integument also has two lateral lobes, which are appressed against each other to form the slit-shaped endostomial part of the micropyle (Fig. 27N). The dorsal side of the funicle in the region of the bend is in close contact with the base of the stylar canal where the PTTT ends and forms a *ponticulus* (Fig. 27A, K, L).

Anatomy: Vascular bundles have a more or less developed resin canal on the dorsal side of the xylem, except for the stamen and ovule bundles (Figs 26, 27). Sepals have a main vascular trace and may have additional lateral bundles forming synlaterals in the short synsepalous region (Fig. 26D, E). Petals have a median and two lateral main vascular traces, which extend along their entire length, and one or two smaller lateral bundles intercalated between the three main ones, which merge basally with the median vascular bundle (Fig. 26A–D). Stamens have a single vascular bundle which splits into two smaller bundles in the upper half of the anther (Fig. 44O). In the carpel, a dorsal vascular bundle with a conspicuous resin canal extends from the stigma down to the ovary base (Fig. 27C–R). Smaller lateral vascular bundles are also present below the stigma and they merge to form a single lateral bundle on each side of the ventral slit (Fig. 27C–I). At the transition from the style to the ovary, the two lateral bundles converge toward the ventral side of the carpel and merge with the median ventral vascular bundle above the ovary (Fig. 27J, K). Lower down, the ventral bundle gives off a branch serving the ovule (Fig. 27L). In the ovary wall, the vasculature forms a network between the dorsal and ventral bundle (Fig. 27M–R). Below the locules, all bundles converge toward the centre of the floral base. They merge with the stamen traces and, lower down, with the petal and sepal traces (Fig. 26D). They form a central stele, in which only the resin canals of the five sepal median traces extend further down (Fig. 26E).

Histology: Stomata are found on the dorsal side of the sepals and petals and more sparsely on the ovary. The stomata tend to be slightly raised on the floral base and the calyx. Lignified and seemingly uniseriate multicellular hairs are sparsely present on the fringed sepal margins. The surface of the nectary disc is slightly papillate and contains nectar pores. Striate cuticular ornamentation is more or less conspicuous on the flower, except for the nectary disc.

Campnosperma squamatum (Anacardiaceae, Spondiadoideae) (Figs 28, 29, 42B, C, 43K, K′, 44P, 46Q, R)

Morphology: The flowers are morphologically bisexual and diplostemonous (Figs 28, 42B, C). They have a tetramerous perianth and androecium and a monomerous gynoecium and they are monosymmetric (Figs 28, 42B, C).

The sepals are basally congenitally united (Fig. 28D, E). Their thick, obtuse free parts have an open aestivation in late bud (Fig. 28C). Petal aestivation is cochlear, but it is basally open (Fig. 28A–D). The petals become longer than the sepals early in development and protect the inner organs up to anthesis (Fig. 28). Postgenital petal coherence is formed between the overlapping margins by interdentation of their papillate surface and striate cuticular ornamentation. At anthesis, the expanded petals are free and erect, except for their tips, which retain the inward inflexion they had in bud (Fig. 42B, C). The inner floral organs remain partially hidden (Fig. 42B, C).

The antepetalous stamens are shorter than the antesepalous ones and have broader and more arrowhead-shaped anthers (Fig. 42B). All stamens have a large and broad filament base, which narrows slightly toward the attachment zone, but are not constricted, and have a slightly X-shaped anther (Figs 42B, 43K, 44P). The anthers are basally dorsifixed with a connective of intermediate thickness and a deep ventral longitudinal furrow (Fig. 44P). Their dorsal side is larger than the ventral side and they are introrse (Fig. 44P). The dehiscence lines extend from the tip of the thecae almost down to their base (Fig. 43K′). Anthers of functionally female flowers are devoid of pollen. A thick and lobed intrastaminal nectary disc is present and surrounds the base of the superior ovary (Fig. 28C).

The position of the single carpel is not clearly antepetalous or antesepalous (Fig. 28B, C). It has a globose ovary, lacks a distinct style and has a thick large discoid stigma, with an irregularly lobed margin (Fig. 46Q, R). The ventral side of the stigma is lower than the dorsal side (Fig. 46Q). The gynoecium is of angiospermy type 4 (Fig. 29). Each carpel is entirely ascidiate up to the base of the stigma (Fig. 29A, D–N). The stigmatic surface is slightly papillate and covered with secretion at anthesis (Fig. 46R). It is unclear whether the papillae are unicellular or partially pluricellular. Below the stigma, the PTTT converges toward the inner angle of the ventral slit and extends to the base of the stylar canal and the placenta (Fig. 29A–K).

The single ovule is crassinucellar, bitegmic and syntropous, with a short and bent funicle inserted apically in the inner angle of the locule (Fig. 29A, I–N). The outer integument is three (four) cell-layers thick and the inner three cell layers. The outer integument is hood-shaped and the inner circular. Both integuments are as long as the nucellus and the micropyle is not closed at anthesis and the nucellus faces the placenta (Fig. 29A, L). In the region of the bend, the dorsal side of the funicle is in close contact with the base of the stylar canal where the PTTT ends and forms a *ponticulus* (Fig. 29A, I). Gynoecia of functionally male flowers are aborted (Fig. 28B, C).

Anatomy: Vascular bundles have a more or less developed resin canal on the dorsal side of the xylem, except for the stamen and ovule bundles (Figs 28, 29). Sepals, petals and stamens have a single vascular bundle, which extends along their entire length (Fig. 28). In the carpel, a median vascular bundle with a conspicuous resin canal extends from the stigma down into the floral base (Fig. 29B–N). At the level of the stigma, vasculature extends laterally on each side of the dorsal bundle and almost forms a continuous arc around the ventral slit (Fig. 29B–D). Lower down, the arc also extends towards the ventral side of the carpel, almost forming a ring in the upper ascidiate zone of the carpel (Fig. 29E–N). Further down, additional peripheral branches and smaller inner bundles without a resin canal form a network around the locule (Fig. 29J–N). A ventral vascular bundle connecting to the ovule is not well differentiated (Fig. 29K). Lower down, the peripheral branches merge with the inner ones and extend with their resin canals into the floral base, where they merge with the traces of the other organs (Fig. 28E).

Histology: Stomata are present on the dorsal side of the petals. Stellate hairs with uniseriate multicellular stalks and multicellular heads are present on the dorsal side of the sepals and petals and the floral base. They are abundant on the ovary, where they occur with multicellular scales (Fig. 46Q). The surface of the nectary disc is slightly papillate and contains nectar pores. Striate cuticular ornamentation is more or less conspicuous on the entire flower, except for the gynoecium.

Anacardium occidentale (Anacardiaceae, Anacardioideae) (Figs 30, 31, 42D, E, 43L, L′, 44Q, 47A–C, 48L–N)

Morphology: The flowers are bisexual and diplostemonous (Figs 30, 42D). Perianth and androecium are pentamerous and the gynoecium is monomerous (Fig. 30). The flowers are thus monosymmetric (Fig. 30).

The sepals are congenitally united for a short length (Fig. 30D). They have a quincuncial aestivation and the two outer sepals are larger than the inner ones (Figs 30A–C, 42E). Petal aestivation is cochlear and shortly open at the base (Fig. 30A–D). The corolla is longer than the calyx in late bud. The floral bud is protected successively by the subtending bract, two prophylls, sepals and petals (Fig. 30). There is no postgenital coherence between the overlapping parts of the protective organs and cohesion in the bud is probably only because of the tight imbrication of the organs (Fig. 30). At anthesis, the petals are reflexed at mid-length above the sepal tips (Fig. 42D). Lower down, their aestivation remains imbricate and they broadly overlap, forming a floral 'tube' with the sepals. The reproductive organs remain hidden except for the single fertile anther and sometimes a stigma (Fig. 42D). The petals have a conspicuous median ridge on the dorsal side of their reflexed part, whereas, below the bend, there is a ridge on the ventral side (Fig. 42D).

There are (8–) 9–10 (–11) stamens (Fig. 30C). All stamens are basally united around the gynoecium (Fig. 47A). However, only the stamen in the radius of the first sepal initiated (plus sometimes a neighbouring stamen) fully develops (Figs 42D, 47A). It becomes conspicuously larger than the other stamens early in development (Figs 30B, 47C). At that time also, the other antesepalous stamens are slightly larger than the antepetalous ones (Fig. 30B), whereas later this difference is no longer present (Fig. 47A). The filaments are round and often have a distal annular thickening just below the sagittate and slightly apiculate anthers (Figs 43L, 44Q). The basal extensions of the thecae are sterile. The anthers are basally dorsifixed (Fig. 43L) and have a broad and thick connective (Fig. 44Q). Their dorsal side is slightly broader than the ventral side and curved backwards around the constricted attachment, which is almost hidden in a pseudopit (Fig. 44Q). The anthers are slightly introrse, almost latrorse and the dehiscence lines extend from the tip of the thecae almost down to where the pollen sac ends (Figs 43L′, 44Q). When the thecae dehisce, the anther tilts and then seems to sit transversally on the filament (Fig. 43L′). Later, it abscises above the annular thickening of the filament, which may function as an abscission zone. There is no intrastaminal nectary disc. In our material, most flowers are functionally male and only a few are bisexual. Only in fertile gynoecia is the style longer than the corolla tube and the longest stamen (Figs 42D, 47A).

The gynoecium is monosymmetric (Figs 30B, C, 31B–N). A single carpel develops on the same radius as

the first sepal (Figs 30B, C, 47C). The flowers thus have an oblique monosymmetry (Fig. 30). The carpel has a globose, laterally flattened ovary and a very long style ending in a small stigma (Figs 31A, 47A, B). The gynoecium is of angiospermy type 4 (Fig. 31). The single carpel is ascidiate up to the base of the style (Figs 31A, G–N, 47C) and plicate further up (Figs 31A–F, 47C). A potential interpretation of the gynoecium as pseudomonomerous is addressed in the Discussion. The locule bulges dorsally and appears curved in a median direction. The stigma is horseshoe-shaped and slightly bilobed (Fig. 31B). It is covered with uniseriate multicellular papillae without noticeable secretion (Fig. 47B). Below the stigma, a PTTT differentiates along the inner angle of the ventral slit and extends into the bulged ceiling of the locule (Fig. 31A–J).

The carpel has a single crassinucellar, pachychalazal, unitegmic and syntropous ovule, with a stout bent funicle inserted basally in the inner angle of the locule (Figs 31A, 48M). The single integument is *c.* 20 cell layers thick and forms a slightly lobed and relatively long micropyle, which is appressed to the floor of the locule, below the insertion of the funicle (Figs 31A, 48N). In addition, the saddle-shaped dorsal side of the funicle–ovule complex is in close contact with the lower end of the PTTT, and they are even postgenitally fused at anthesis, thus forming a *ponticulus* (Figs 31A, I, J, 48L, M).

Anatomy: Vascular bundles have a more or less developed resin canal on the dorsal side of the xylem, except for the stamen and ovule bundles (Figs 30, 31). Sepals have one median vascular bundle and two to four main lateral bundles (depending on sepal breadth: outer sepals are broader than inner ones), which extend along their entire length (Fig. 30A–D). Additional, smaller bundles are present and a sepal can have up to 11 bundles. In the synlateral zone, the main laterals do not form synlaterals (Fig. 30D). Petals have a median and two main lateral vascular bundles, which extend almost along their entire length (Fig. 30A–C). They fuse at the base of the petal (Fig. 30D). Additional smaller lateral bundles toward the petal margins are also present. A petal can have up to seven bundles. Stamens have a single vascular bundle (Fig. 44Q). In the carpel, a large dorsal and two smaller main lateral vascular bundles are present below the stigma (Fig. 31C). Additional lateral bundles appear lower down (Fig. 31D–F) and, in the upper end of the ovary, the dorsal and lateral bundles form an arc of vasculature on the dorsal side of the carpel (Fig. 31G). In the ovary wall, the arc of vasculature becomes thicker and comprises resin canals (Fig. 31H). Its two lateral branches expand toward the ventral side of the locule (Fig. 31I). The arc almost forms a continuous ring around the locule and resin canals are no longer present (Fig. 31I–M). At the base of the locule, a ventral median vascular bundle branches off from this band and serves the ovule (Fig. 31L–N). In the chalaza, the ovule bundle forms *c.* eight smaller bundles, which extend into the integument (Fig. 31I–M).

Histology: Stomata are present on the dorsal side of the sepals and petals and along the style. They are slightly raised on sepals and petals. An indument of unicellular hairs covers both sides of distal parts of the sepals and petals. It is restricted further down to their dorsal side and the floral base. Similar hairs are also found on the filament of the (two) longest stamen(s) and at the base of the style on the dorsal side of the ovary (Fig. 47A). There is no nectary disc. However, on the lower half of the petals, there are ventral ridges, which have an apparently secretory epidermis. In addition, secretory hairs with uni- or bicellular stalks and multicellular heads are clustered between the petal bases and the androecial tube.

Mangifera indica (Anacardiaceae, Anacardioideae) (Figs 32, 33, 42F–H, 43M, M′, 44R, 47D–G)

Morphology: Flowers are morphologically bisexual and appear haplostemonous (Figs 32, 42G, 47G). Perianth and androecium are pentamerous and the gynoecium is monomerous (Figs 32, 42G, 47G).

Sepal aestivation is quincuncial and the two outer sepals are larger than the inner ones. Petal aestivation is cochlear or contort (Figs 32, 42F). The corolla becomes longer than the calyx in bud and protects the reproductive organs up to anthesis (Figs 32, 42F). There is no postgenital coherence between the overlapping parts of the protective organs and cohesion in bud is probably only because of the regular aestivation of the organs (Fig. 32). At anthesis, the expanded sepals and petals are free for their entire length and reflexed. The reproductive organs are entirely exposed. The lower half of the petals has secretory ridges on the ventral side, whereas the distal part and the margins are reflexed (Figs 32, 42G, H, 47G). Between the narrow petal bases, there are five broad and thick extrastaminal nectary lobes (Figs 32C, D, 42G, 47G).

The stamens are unequally developed (Figs 32B, 47G). At anthesis, only the stamen on the radius of the first sepal is fertile and much larger than the other stamens, which are reduced to staminodes (Figs 42G, 47G). The fertile stamen has a broad and thick filament base, which becomes rounder and narrows toward the constricted tip (Fig. 43M). The anther is slightly X-shaped. It is dorsifixed at mid-length and

the attachment zone is hidden in a pseudopit formed by the dorsal side of the thecae (Figs 43M, 44R). It has a broad and thick connective and a deep ventral and a dorsal longitudinal furrow (Fig. 44R). The dorsal side is larger than the ventral side and the anther is introrse (Fig. 44R). The dehiscence lines extend from the tip of the thecae down to the base furrow (Fig. 43M′). An intrastaminal nectary disc is missing.

The gynoecium is monosymmetric (Figs 32B, C, 33B–N). The position of the single carpel is not fixed. It can be antesepalous or antepetalous, which often leads to a mismatch of the gynoecium symmetry plane and that of the perianth plus androecium (Fig. 32R). Only when the carpel develops on the radius of the fertile stamen is the flower really monosymmetric, but with an oblique symmetry plane. Each carpel has a globose ovary and a long style ending in a small stigma (Figs 33A, 47D–G). The gynoecium is of angiospermy type 4 (Fig. 33). It is ascidiate up to the base of the style (Fig. 33A, I–N) and plicate further up (Fig. 33A–G). A potential interpretation of the gynoecium as pseudomonomerous is addressed in the Discussion. The stigma is short and horseshoe-shaped and has a papillate surface without apparent secretion (Figs 33A–D, 47F). Below the stigma, a PTTT differentiates along the inner angle of the ventral slit and extends downwards. It forms large papillae extending from the base of the stylar canal into the locule (Fig. 33A–M).

The carpel has a single crassinucellar, pachychalazal, unitegmic and syntropous ovule, with a stout bent funicle inserted basally in the inner angle of the locule (Fig. 33A). The single integument is *c.* 15 cell layers thick and forms a lobed micropyle, which is imperfectly closed at anthesis. The saddle-shaped dorsal side of the funicle–ovule complex is in close contact with the lower end of the PTTT and may form a *ponticulus* (Fig. 33A, K–M). Only after anthesis are they postgenitally fused.

Anatomy: Vascular bundles have a more or less developed resin canal on the dorsal side of the xylem, except for the stamen and ovule bundles (Figs 32, 33). Sepals have a median vascular bundle, which extends along their entire length, and, depending on their position, one or two shorter lateral bundles, which merge with the median one at the base, and there is one vascular trace (Fig. 32C–E). Petals have a median and two main lateral vascular bundles, which extend almost along their entire length (Fig. 32C). Additional smaller lateral bundles are present and petals may have up to eight bundles in the distal part (Fig. 32B). The main lateral bundles merge with the median bundle only in the floral base, where there is a single vascular trace (Fig. 33D, E). Stamens have a single vascular bundle (Fig. 44R). In the carpel, a massive lateral vascular bundle is present below the stigma on each side of the ventral slit (Fig. 33D–I). The dorsal bundle is weak and the lateral bundles extend into the ventral side of the ovary wall. The weak dorsal vascular bundle extends downwards into the base of the style (Fig. 33E–I); in the ovary it is connected with ovary wall bundles (Fig. 33I–N). These form two layers of numerous bundles around the locule, an inner and an outer (Fig. 33J–N). All bundles merge below the ovary and form a single central ring of vasculature which branches, forming an inner median ventral bundle serving the ovule. In the chalaza, the ovule bundle gives off several branches, which extend into the integument.

Histology: Few stomata are present on the dorsal side of sepals and petals. Unicellular lignified and non-lignified hairs are sparsely present on the sepals and floral base. The sepal margins are sparsely fringed, whereas those of the petals are finely lacerate. The surface of the nectary lobes is irregularly cleft (Fig. 47G), with nectar pores at the base of the clefts. The ridges on the ventral side of the petals have a conspicuously stained epidermis, which is probably also secretory, but does not have pores. Striate cuticular ornamentation is more or less conspicuous on the entire flower.

Blepharocarya involucrigera (Anacardiaceae, Anacardioideae) (Figs 34, 35, 42I, 43N, N′, 44S, 47H, I)

Morphology: Flowers are morphologically bisexual or female and strongly dimorphic. The morphologically bisexual flowers are diplostemonous, with a tetramerous perianth and a monomerous gynoecium. Female flowers lack stamens and the perianth is somewhat irregular in organ number (Fig. 34).

The sepals are congenitally united at the base. In morphologically bisexual flowers, they have acute erect tips, with an open aestivation, whereas, in female flowers, their free parts are longer and have an imbricate aestivation (Fig. 34A–D). Petal aestivation is slightly imbricate or induplicate–valvate, but open at the base (Fig. 34A–D). The flowers remain packed in cupular inflorescences up to anthesis and in bisexual flowers the petals only become longer than the sepals in bud. At anthesis, female flowers remain tightly packed in the cupular inflorescences and only the stigmas are exerted through the sepals and petals, which are of almost the same length (Fig. 42I). In contrast, the pedicel of the bisexual flowers elongates before anthesis and the flowers open above the cupule. The petals are free and have an open aestivation, but are erect and longer than the reproductive organs, which are only partly exposed.

The antepetalous stamens are shorter than the antesepalous ones at all stages of development. All stamens have a broad and thick filament base, which narrows slightly toward the constricted tip, and an X-shaped anther (Fig. 43N). The anthers are basally dorsifixed and have a thin and narrow connective and a deep ventral and a dorsal longitudinal furrow (Fig. 44S). Their dorsal side is larger than the ventral side and the anthers are slightly introrse (Fig. 44S). The dehiscence lines extend from the tip of the thecae almost down to their bases (Fig. 43N′). In female flowers, remnants of highly reduced stamens are sometimes present on the petal radii. A thick lobed intrastaminal nectary disc is present in bisexual flowers, whereas in female flowers it is smaller and is located between the petal and gynoecium bases.

In all flowers, the single carpel is antesepalous (Fig. 34). The gynoecium and thus the flower are monosymmetric (Fig. 34). The ovary is slightly flattened laterally and the style is as long as the ovary and ends in a small stigma (Figs 35, 47H). The shape of the gynoecium may vary slightly depending on the position of the flowers within the inflorescence. The gynoecium is of angiospermy type 4 (Fig. 35). The carpel is ascidiate for half the length of the ovary (Fig. 35A, G–K) and plicate further up (Fig. 35A–F). A ventral longitudinal furrow extends from the base of the stigma almost down to the ovary base. At the base of the style, the furrow is deeper and the margins of the carpels are somewhat protruding (Figs 34C, 35A, E). They may be interpreted as the remnants of two smaller carpels or as secondary formation (see Discussion). The stigma has long unicellular papillae, which collapse at anthesis and are covered with secretion (Fig. 47I). Below the stigma, a PTTT differentiates along the inner angle of the ventral slit and extends downwards into the base of the stylar canal (Fig. 35A–F). It does not appear to connect to the placenta.

The carpel has a single crassinucellar, unitegmic, anatropous and syntropous ovule, with a bent funicle inserted more or less basally in the inner angle of the locule (Figs 35, 47H). The single integument is four to five cell layers thick. It is hood-shaped and much longer on the convex than on the concave side. It has two large lateral flaps, which are wrapped around the funicle and the nucellus (Fig. 35G–I). The micropyle is slit-shaped. In the region of the bend, the dorsal side of the funicle–ovule complex is in close contact with the base of the stylar canal, where the PTTT ends, and forms a *ponticulus* (Fig. 35A, F).

Anatomy: Vascular bundles have a more or less developed resin canal and a ventral xylem, except in stamens, carpels and ovules (Figs 34, 35). Sepals have a median vascular bundle, which extends along their entire length, and, depending of their position, a shorter lateral bundle, which merges with the median one at the base (Fig. 34). Petals have a median and two main lateral vascular bundles, which extend almost along their entire length, and one trace. Stamens have a single vascular bundle, which may split into two branches in the distal part of the anther (Fig. 44S). In the carpel, a dorsal vascular bundle extends from the stigma to the ovary (Fig. 35B–K). In the lower part of the style, two shorter lateral bundles differentiate on each side of the ventral slit (Fig. 35E). In the upper end of the ovary, the laterals extend toward the ventral side of the carpel (Fig. 35F). Below the placenta they merge and form a ventral bundle, a branch of which forms the ovule bundle (Fig. 35G–I). Further down, the ventral and dorsal vascular bundles extend into the floral base, where they merge together with the other vascular traces and form a central vascular complex (Fig. 34E).

Histology: Stomata are present on the dorsal side of the sepals. In male flowers, unicellular lignified hairs are present on the floral base and the dorsal side of sepals and petals and on the margins of the sepals. Longer lignified and seemingly uniseriate, multicellular hairs are found on the nectary disc and the carpellode. In female flowers, both types of lignified hairs are present on the floral base and the dorsal side of the sepals, but less so on petals, ovary and base of the style (Fig. 47H). Glandular hairs with uniseriate multicellular stalks and multicellular heads are also present on the dorsal side of the sepals. In male flowers, the nectary disc is slightly papillate, whereas, in female flowers, where it remains hidden, it is smooth. In both male and female flowers, the disc contains nectar pores. In both male and female flowers, a striate cuticular ornamentation is more or less conspicuous on the entire flower.

Schinus molle (Anacardiaceae, Anacardioideae) (Figs 36, 37, 42J, 43O, O′, 44T, 47J–L, 48O–Q)

Morphology: Flowers are morphologically bisexual, diplostemonous and pentamerous, with a trimerous gynoecium (Figs 36, 37H). The sepals are more or less congenitally united at the base (Fig. 36D). Their free parts have a quincuncial aestivation in very young buds, with the two outer sepals slightly larger than the inner ones. Petal aestivation is cochlear, sometimes quincuncial, but open at the base (Fig. 36A–C). The petals become longer than the sepals in the bud and protect the inner organs up to anthesis (Fig. 36). Postgenital coherence between the petals is formed by

interdentation of their papillate surface and cuticular ornamentation. At anthesis, the sepal tips are obtuse. They have an open aestivation, although their margins may still slightly overlap basally. The expanded petals are free for their entire length and are distally slightly recurved. They have an open aestivation, except at mid-length, where they are still imbricate (Fig. 42J). They are longer than the inner floral organs, which remain partly hidden (Fig. 42J).

The antepetalous stamens are shorter than the antesepalous stamens throughout development. All stamens have a broad flattened filament base, which becomes rounder and narrower towards the constricted tip, and a slightly X-shaped anther (Figs 43O, 44T). The anthers are basally dorsifixed and may be versatile. They have a thin and narrow connective and a deep ventral and a deep dorsal longitudinal furrow (Fig. 44T). Their dorsal side is not much larger than the ventral side and the anthers are almost latrorse. Distally they are slightly introrse (Fig. 44T). The dehiscence lines extend from the tip of the thecae down to their bases and encompass the lower shoulders (Fig. 43O′). In our material, either male or female organs are sterile and the flowers are thus functionally unisexual. A thick lobed intrastaminal nectary disc surrounds the base of the gynoecium.

The syncarpous gynoecium has a globose superior ovary and lacks a distinct style (Figs 37A, 47J). Three stigmatic branches, each with a ventral longitudinal furrow, extend from the base up to the slightly bilobed capitate stigma (Fig. 47K). The branches are radially arranged and the gynoecium appears thus polysymmetric at first sight (Fig. 47J). However, one of the three carpels becomes larger than the other two early in development (Fig. 47L) and develops a fertile locule and ovule at anthesis (in functionally female flowers). The other two carpels lack a locule and ovule. They are reduced and form only styles and stigmas, which are similar in shape to those of the fertile carpel (Fig. 47J). The gynoecium is thus pseudomonomerous and monosymmetric, but the position of the fertile carpel appears to be variable (Figs 36, 37). It is either antesepalous or antepetalous (or in between) and may lead to a mismatch of the symmetry plane of the gynoecium with that of perianth plus androecium. When the flowers are monosymmetric, the symmetry plane is oblique. The gynoecium is of angiospermy type 4 (Fig. 37). The unilocular ovary appears 'asciidiate' (but see Discussion) and the gynoecium is synascidiate above the locule (see Discussion) (Fig. 37A, E, F). At the base of the stigmatic branches, it may have a short symplicate transition zone below the apocarpous zone (Figs 36C, 37A, D). The stigmas have uniseriate multicellular papillae, which are covered with secretion at anthesis (Fig. 47K). Below the stigmas, the PTTTs differentiate along the inner angle of the ventral slit of each carpel (Fig. 37A, C, D). They extend separately into the synascidiate part and may form a compitum at the base of the stylar canal before they reach the placenta (Fig. 37A, F, G).

The fertile carpel has a single crassinucellar, bitegmic, anatropous and syntropous ovule, with a bent funicle inserted almost apically in the inner angle of the locule (Fig. 37A). It is asymmetric and its shape is reminiscent of a sea slug (Fig. 48O–Q). Both integuments are three cell-layers thick but the outer integument appears thicker than the inner. The inner integument is twice as long as the nucellus, but shorter than the outer integument (Fig. 37A–K). It is chimney-like around the nucellus and forms a slit-shaped endostome (Fig. 37A). The outer integument is hood-shaped with two large lateral flaps unequally developed and loosely folded around the inner integument and nucellus (Fig. 37A, I–K). It forms an irregularly lobed slit-shaped micropyle (Fig. 48Q). In addition, in the region of the bend, the dorsal side of the funicle–ovule complex is in close contact with the base of the stylar canal where the PTTT ends and may form a *ponticulus* (Figs 37A, F, 48O, P).

Anatomy: Vascular bundles have a more or less developed resin canal and a ventral xylem, except in stamens and ovules (Figs 36, 37). Sepals have a median vascular bundle, which extends along their entire length, and two main shorter lateral bundles, which form synlaterals in the floral base (Fig. 36C–E). Petals also have a single median vascular bundle at the base (Fig. 36C). Further up, it gives off smaller lateral bundles, which may also branch and form additional lateral vascular bundles (Fig. 36A, B). A petal can have up to ten bundles. Stamens have a single vascular bundle (Fig. 44T). In the carpels, two lateral vascular bundles are present below the stigma (Fig. 37C) and, only in the fertile carpel, a dorsal bundle differentiates lower down (Fig. 37D). In the upper part of the style, the laterals of each sterile carpel merge over their ventral side and form an arc of vasculature (Fig. 37E). These two arcs extend along the ventral slit of the fertile carpel and merge downwards with its vasculature, forming together a larger arc of vasculature above the locule, with a pair of vascular bundles at the ventral end of the arc (Fig. 37E). This network forms a ventral branch, which serves the ovule (Fig. 37G, H). Further down in the ovary wall, conspicuous large cavities differentiate in the vasculature, which are interpreted here as very large resin canals (Fig. 37F–L). They end below the locule and the vasculature of the gynoecium extends as a small ring into the floral base (Figs 36D, 37M), whereas the dorsal resin canals of the perianth traces are still conspicuous (Fig. 36D, E). The synlat-

eral traces of the sepals merge with the petal plus stamen traces on the same radii (Fig. 36E). In the floral base, all resin canals merge into two or three much larger resin canals.

Histology: Few stomata are present on the dorsal side of the flower and sepal bases. The flowers are glabrous, except for the fringed margins of the sepals. The nectary disc is smooth and contains nectar pores. Striate cuticular ornamentation is present almost all over the flower and is especially conspicuous on anthers.

Semecarpus riparius (Figs 38, 39, 42L, 47M, N) and *S. australiensis* (Fig. 42K, 43P, P′, 44U) (Anacardiaceae, Anacardioideae)

Morphology: Flowers are morphologically bisexual, haplostemonous and pentamerous, with a trimerous gynoecium (Fig. 42K, L). Sepals are shortly congenitally united (Fig. 38D). They already have an open aestivation in young buds but may give a slightly quincuncial impression in the united base (Fig. 38D). Petal aestivation is contort or cochlear (Fig. 38A–C). Petals become longer than the sepals in young buds and protect the inner organs up to anthesis (Fig. 38). Postgenital coherence between the petals is formed by interdentation of their cuticular ornamentation. At anthesis, the free parts of the sepals are obtuse with an open aestivation. The expanded triangular and obtuse petals are recurved and have ventral longitudinal ridges toward the base (Fig. 42K, L). The inner floral organs are completely exposed (Fig. 42K, L).

The stamens have a flattened filament base, which becomes rounder and narrows towards the constricted tip, and a pronouncedly sagittate anther (Figs 43P, 44U). The anthers are dorsifixed at mid-length (Fig. 43P). They may be versatile and are caducous. They have a thin and narrow connective and a deep ventral longitudinal furrow (Fig. 44U). Their dorsal side is distally larger than the ventral side and the anthers are introrse (Fig. 44U). The dehiscence lines extend from the tip of the thecae almost down to their bases and do not encompass the lower shoulders (Fig. 43U). In our material, the flowers are functionally unisexual. An intrastaminal nectary disc is present in all flowers and covers the base of the gynoecium.

The syncarpous gynoecium comprises a semi-inferior ovary and lacks a distinct style (Fig. 39A). It has three stigmatic branches with a ventral longitudinal furrow, which extend from their base up to the slightly bilobed stigmas (Fig. 47M, N). The branches are regularly radially arranged and the gynoecium appears polysymmetric at first sight (Fig. 47M). However, one of the three carpels becomes larger. The other carpels lack a locule and ovule and their stigmatic branches may be slightly smaller. The gynoecium is thus pseudomonomerous and monosymmetric (Fig. 39). The position of the fertile carpel tends to be antesepalous, but may also have other positions, and leads to a mismatch of the symmetry plane of the gynoecium with those of the other parts of the flower. When the flower is monosymmetric, the symmetry plane is oblique. The gynoecium is of angiospermy type 4 (Fig. 39). The unilocular ovary appears 'ascidiate' (but see Discussion) and the gynoecium is synascidiate above the locule (see Discussion). Below the plicate zone of the carpels, there is a short symplicate transition zone and a compitum may be present (Figs 38B, 39C). The stigmas have uniseriate multicellular papillae, which are covered with secretion at anthesis (Fig. 47N). Below the stigmas, the PTTTs differentiate along the inner angle of the ventral slit of each carpel (Fig. 39A). They extend separately into the symplicate region and lower into the synascidiate part (Fig. 39A, C, D). At this level they do not seem to form a compitum, as the PTTT of the sterile locules ends in the synascidiate zone and only the PTTT of the fertile carpel appears to reach the base of the stylar canal and placenta (Fig. 39A, E, F).

The fertile carpel has a single crassinucellar, slightly campylotropous and syntropous ovule, with a short bent funicle inserted apically in the inner angle of the locule (Fig. 39A). In *S. australiensis*, one integument appears to be present in the median plane (11 cell layers present at mid-length), but two integuments in the transversal plane (6–7 cell layers in the outer integument and 4–5 in the inner one). This corresponds to a perichalazal structure. In *S. riparius*, only one integument (*c.* 12 cell layers thick) is evident (Fig. 39A), but there are irregular lateral flaps at the raphe, which may correspond to a second (outer) integument (Fig. 39A, H, I). In *S. riparius*, the ovule is inserted higher up in the locule than in *S. australiensis*. At anthesis, the micropyle is entirely closed in *S. riparius* (Fig. 39A), but not in *S. australiensis*. In both species, the dorsal side of the funicle–ovule complex is in close contact with the lower end of the PTTT at the base of the stylar canal and may form a *ponticulus* (Fig. 39A, F, G).

Anatomy: Vascular bundles have a more or less developed resin canal on the dorsal side of the xylem, except for the stamen and ovule bundles (Figs 38, 39). Sepals have a median vascular bundle, which extends along their entire length and up to five lateral vascular bundles on each side (Fig. 38C). The lateral-most bundles form synlaterals in the short synsepalous region and extend into the floral base (Fig. 38C). Each sepal has more than three vascular traces. Petals have a median vascular bundle, which extends along their

entire length, and up to 35 lateral vascular bundles (Fig. 38A, B). In the petal base, the lateral vascular bundles merge successively with the median vascular bundle and they form a single trace in the floral base (Fig. 38C, D). Stamens have a single vascular bundle, which bifurcates in the distal region of the anthers (Fig. 44U). In the carpels, there is a dorsal vascular bundle without a resin canal below the stigma and two lateral bundles with a conspicuous resin canal (Fig. 39B). In the short symplicate zone, the lateral bundles of the fertile carpel and the adjacent lateral bundles of the sterile carpels form synlaterals (Fig. 39C, D), whereas no synlateral is formed between the sterile carpels (Fig. 39D). In the synascidiate part of the style, the vasculature becomes reticulate around each carpel (Fig. 39D) and forms lower down a thick band of vascular tissue with numerous resin canals around the periphery of the ovary wall (Fig. 39E–M). In the upper end of the locule, a median ventral bundle branches off and serves the ovule. Below the locule, the vasculature of the gynoecium extends as a small ring into the floral base, where it merges with the traces of the outer floral organs (Fig. 39M).

Histology: Stomata are present on the dorsal side of the petals and anthers (slightly raised on the anthers in *S. riparia*). A dense indument is present on all floral organs, except for the stigmatic branches and the ventral side of sepals, petals and anthers (Fig. 47M). It consists of long, seemingly unicellular hairs and sparse uniseriate multicellular glandular hairs. The hairy nectary surface contains nectar pores. Striate cuticular ornamentation occurs on the entire flower and is especially conspicuous on the anthers.

DISCUSSION

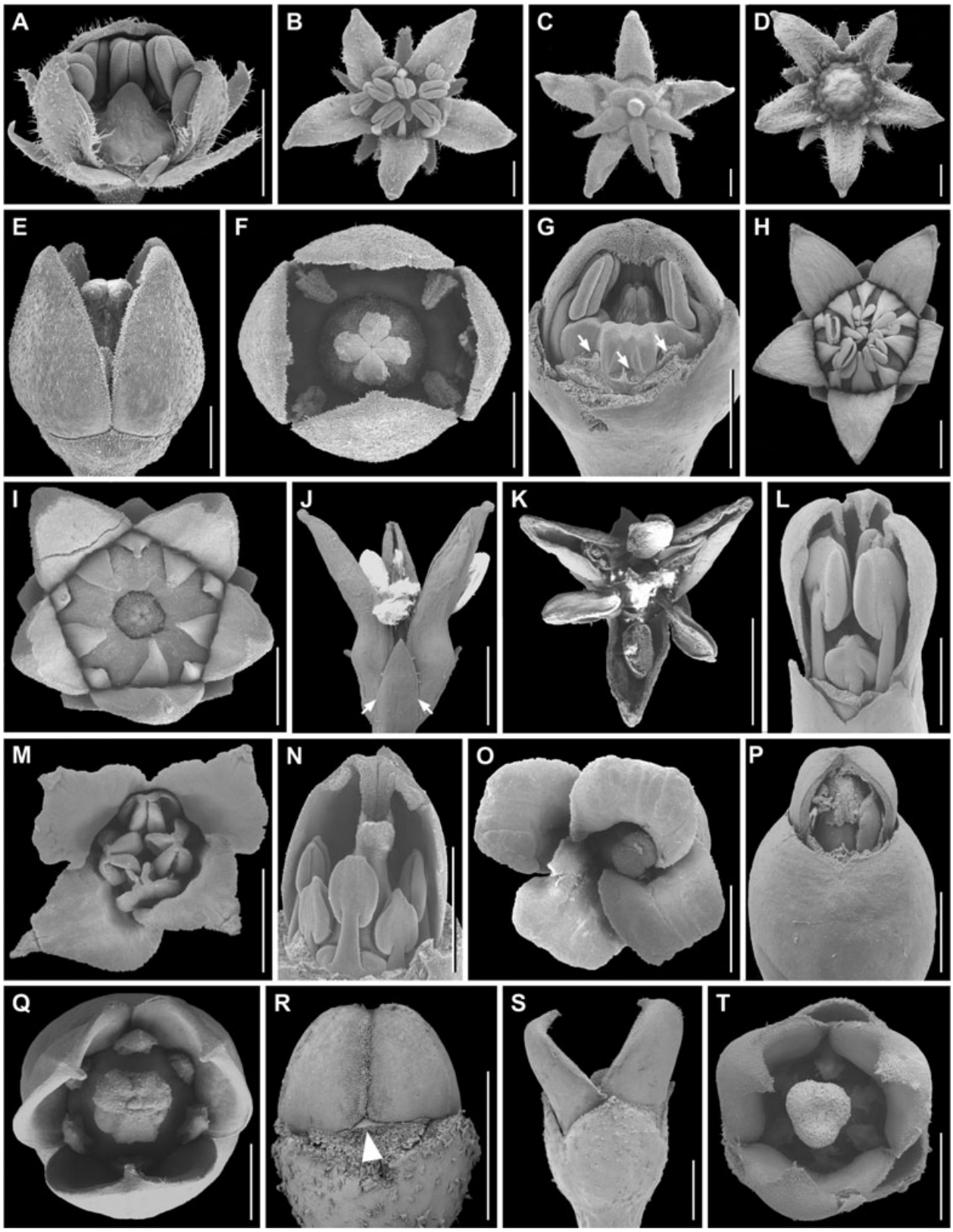
Comparative floral strcuture

General floral structure and biology

The presence of relatively small (mostly less than 1 cm), morphologically bisexual, entomophilous flowers with a thick, lobed (intrastaminal) nectary disc is widespread in Anacardiaceae and Burseraceae (Figs 40–42) (this study; Engler, 1892, 1896; Daly, 1997; Ding Hou, 1978; Mitchell, 1995, 1997). Most flowers are bowl-shaped and the corolla is commonly widely open at anthesis, especially in Anacardiaceae. In contrast, strongly dimorphic, unisexual flowers, with the nectary disc reduced or lacking are rare and have been reported only in few wind-pollinated taxa in Anacardioideae (*Pistacia* L., former Julianiaceae, Dobineeae; Bachelier & Endress, 2007; Pell & Mitchell, 2007). In addition, such wind-pollinated taxa tend to have a reduced perianth. The corolla is missing in *Pistacia* and the female flowers completely lack a perianth in former Julianiaceae and Dobineeae (Anacardioideae) (Jadin, 1894; Forman, 1954; Bachelier & Endress, 2007).

The morphologically bisexual flowers are functionally unisexual in almost all Anacardiaceae and Burseraceae, including all species studied here (in *Anacardium* L. and *Bursera*, functionally bisexual flowers appear to be present as well). The plants are monoecious or dioecious, with a broad range of intermediate forms (Engler, 1892, 1897; Ding Hou, 1978; Wannan & Quinn, 1991; Mitchell, 1995; Daly, 1997; Mitchell, 1997). The distribution of male and female flowers may vary within an inflorescence and follow a regular pattern, as in *Anacardium* (Copeland, 1961; Moncur & Wait, 1986; Moncur, 1988). Bisexual, func-

Figure 40. Flower buds and anthetic flowers; Burseraceae ('male' or 'female' is meant in a functional and not morphological sense). A–D, *Beiselia mexicana*. A, male flower bud, lateral view, one petal and three stamens removed, nectary disc and reduced gynoecium. B–C, anthetic male flower. B, from above. C, from below. D, anthetic female flower, from above. E–F, *Protium morii*, anthetic female flower. E, lateral view, stigmatic head between the petals. F, from above, carpels antepetalous. G–I, *Protium obtusifolium*. G, male flower bud, lateral view, one sepal, two petals and three stamens removed, insertion level of antesepalous stamen lower than that of antepetalous stamens (arrows). H, anthetic male flower, from above, antepetalous stamens appearing longer than antesepalous stamens (because of their higher insertion level). I, early anthetic male flower, anthers removed, five reduced antepetalous carpellodes in centre of nectary disc. J–K, *Bursera* sp., anthetic flower. J, lateral view, floral cup with free sepal margins (arrows). K, from above, petals folded around antepetalous stamens. L–O, *Commiphora caudata*. L, male flower bud, lateral view, one petal removed, antepetalous stamens shorter than antesepalous stamens. M, anthetic male flower, from above, imbricate petal aestivation, antesepalous stamens. N, female flower bud, lateral view, three sepal tips and two petals removed, antepetalous stamens shorter and with more pronouncedly apiculate anthers than in antesepalous stamens, carpel tips connected with two remaining valvate petal tips, which are bent inwards and are postgenitally coherent. O, anthetic female flower, from above, imbricate petal aestivation, two antepetalous carpels. P–Q, *Canarium caudatum*. P, female flower bud, one petal removed, valvate aestivation of postgenitally coherent petals, with tips bent inwards and connected with the carpel tips. Q, anthetic female flower, from above, three antepetalous carpels. R–T, *Santiria* cf. *apiculata*. R, female flower bud, lateral view, sepal free parts removed, petals valvate but aestivation slightly open at the base (arrowhead). S–T, anthetic female flower. S, lateral view, petals with tips bent inwards. T, from above, three antepetalous carpels. Scale bars, 1 mm (A–Q); 500 μm (R–T).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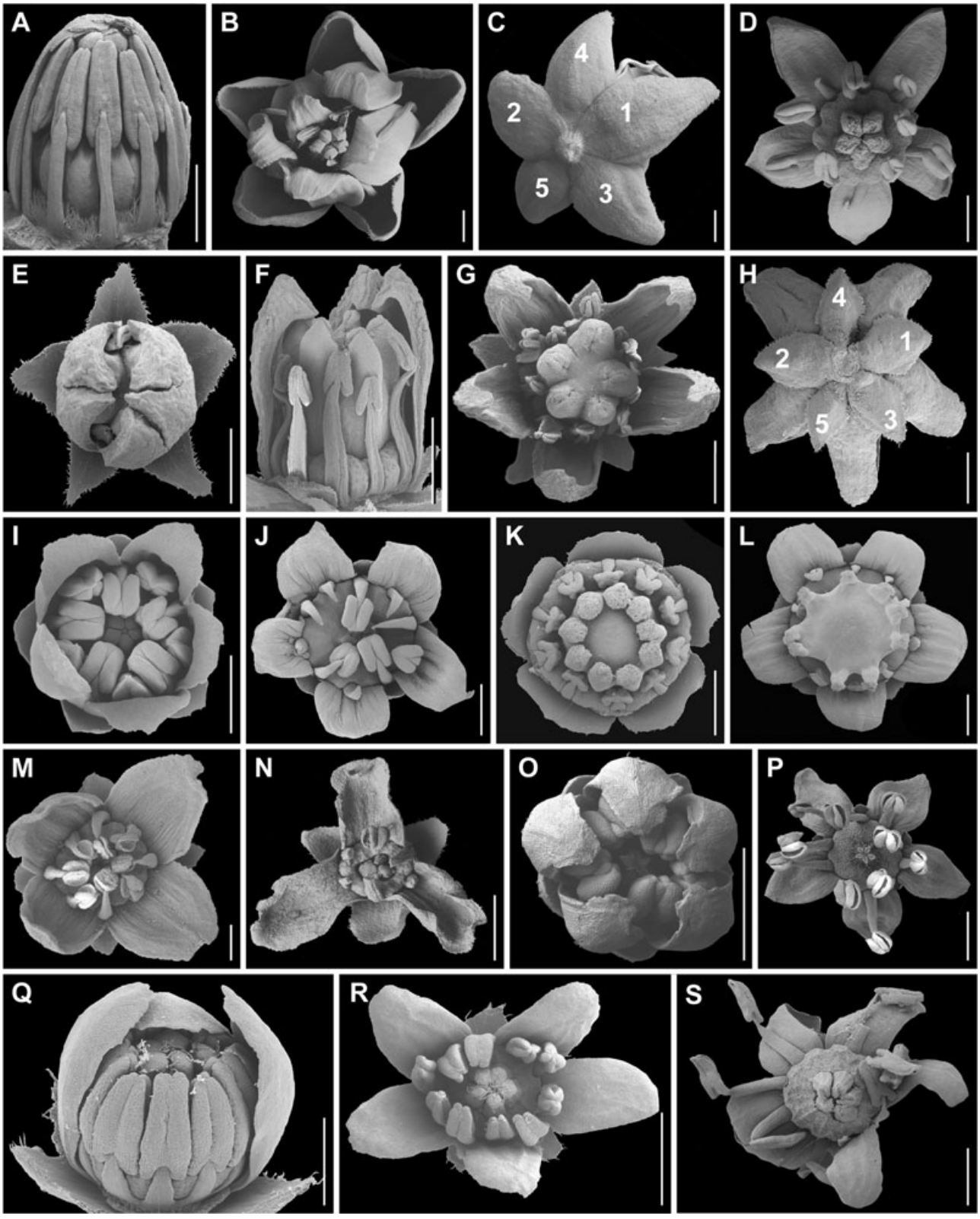
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Figure 41. Flower buds and anthetic flowers; Anacardiaceae, Spondiadoideae ('male' or 'female' is meant in a functional and not morphological sense). A–C, *Dracontomelon dao*. A, flower bud, lateral view, three sepals and two petals removed, fringed lobes of nectary disc between filament bases, antepetalous stamens smaller than antesepalous ones. B–C, anthetic flower. B, from above, petal tips curled backwards, some anthers, carpels antepetalous. C, from below, sepal sequence numbered. D, *Spondias dulcis*, anthetic female flower, from above, petals recurved, carpels antepetalous. E–H, *Spondias purpurea*. E–F, female flower bud. E, from above, sepals with fringed margins, petals valvate. F, lateral view, two petals removed, antepetalous stamens shorter and smaller than antesepalous ones, valvate petal tips hooded. G–H, late anthetic female flower. G, from above, the antepetalous carpels have their tips slightly displaced after anthesis and appear almost antesepalous. H, from below, sepal sequence numbered. I–L, *Pleiogynium solandri*. I, male opening flower, from above, petals imbricate, antepetalous stamens shorter and smaller and with more pronouncedly apiculate anthers than antesepalous ones, carpellodes antepetalous. J, anthetic male flower, from above, recurved petals with longitudinal ridges, anthers apparently caducous. K, early anthetic female flower, from above, all petals removed, gynoecium with nine contiguous carpel tips. L, late anthetic female flower, from above, recurved petals with longitudinal ridges, gynoecium with nine carpel tips more recurved. M, *Pseudospondias microcarpa*, anthetic male flower, from above, nectary lobes between stamen filament bases. N, *Pseudospondias longifolia*, anthetic male flower, from above, carpellodes antepetalous. O–P, *Tapirira* sp. O, male opening flower, antesepalous anthers between petals. P, anthetic male flower, carpellodes antepetalous. Q–S, *Buchanania arborescens*. Q, flower bud, lateral view, two petals removed, imbricate petal aestivation, nectary lobes between stamen bases. R, early anthetic female flower, from above, carpels antepetalous. S, anthetic female flower, petals recurved, sterile stamens with caducous anthers, lobed nectary disc surrounding the antepetalous carpels. Scale bars, 1 mm (A–L, S); 500 μm (M–R).

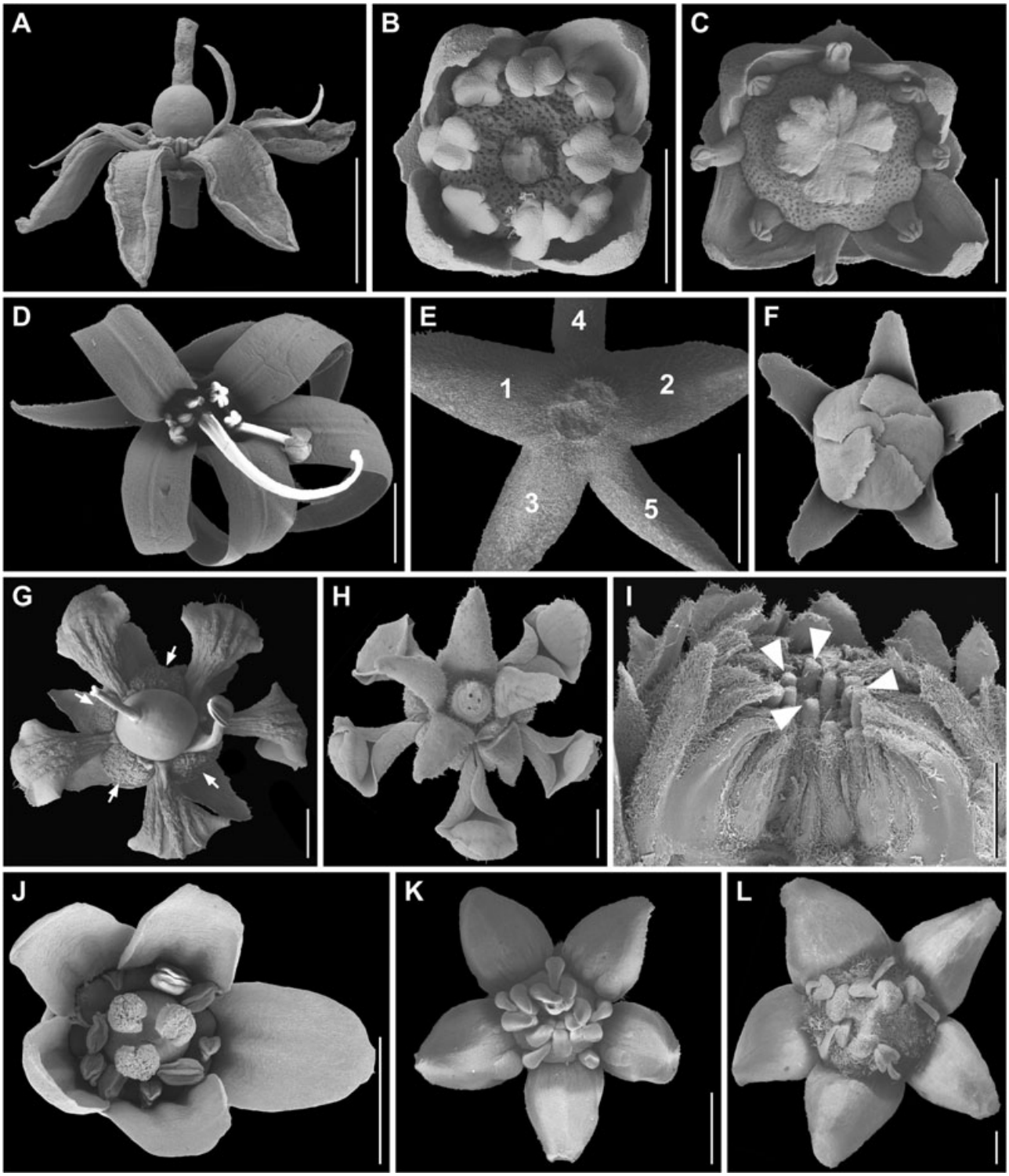
tionally female flowers are reported to be larger than functionally male flowers in both families, in *Anacardium* (Wunnachit, Jenner & Sedgley, 1992) and *Antrocaryon* Pierre (Engler, 1900) in Anacardiaceae and *Protium* Burm. f. (Daly, 2007) in Burseraceae. In some genera of Anacardiaceae, dioecy is associated with strong floral dimorphism (*Pistacia*, Bachelier & Endress, 2007) or inflorescence dimorphism (*Amphipterygium* Schiede ex Standl., Bachelier & Endress, 2007; *Blepharocarya* F. Muell., Wannan *et al.*, 1987; *Laurophyllus* Thunb., Wannan & Quinn, 1992).

Entomophilous flowers with a nectary disc are common in Sapindales. Wind pollination has been reported in *Leitneria* Chapm. (Simaroubaceae) (Trelease, 1894; Stone, 1973) and *Acer* L. *p.p.* and *Dodonaea* Mill. (Sapindaceae) (de Jong, 1976; Hesse, 1979; Endress & Stumpf, 1991). Patterned distribution of functionally male and female flowers within an inflorescence also occurs in other Sapindales such as *Kirkia* Oliv. (Kirkiaceae) (Bachelier & Endress, 2008), *Cupania* L. (Sapindaceae) (Bawa, 1977) and *Cedrela* P. Browne, *Melia* L. and *Toona* (Endl.) M. Roem. (Meliaceae) (Styles, 1972; Gouvêa, Dornelas & Martinelli, 2008a; Gouvêa, Dornelas & Rodriguez, 2008b). In addition, several taxa exhibit heterodichogamy, as reported in *Kirkia* (Kirkiaceae) (Immelman, 1984; Bachelier & Endress, 2008) and *Acer* and *Cupania* (Sapindaceae) (Gabriel, 1968; de Jong, 1976; Bawa, 1977; Tatsuhiro, 2000; Sato, 2002; Gleiser & Verdú, 2005; Renner *et al.*, 2007; Kikuchi & Shibata, 2008).

Floral merism and symmetry

Floral merism is variable at the familial level. Isomerous, trimerous to pentamerous, polysymmetric flowers are common in both families (in Anacardiaceae, mainly Spondiadoideae). They are more frequently pentamerous in Anacardiaceae (Spondiadoideae, Figs 41, 42) and trimerous in Burseraceae (Canarieae, Fig. 40) (this study; Baillon, 1874a; Lam, 1932a, b; Endress, 1996). In both families, there are groups that deviate in the merism of the gynoecium, more rarely in the androecium (see below). In some Anacardioideae, published illustrations (Payer, 1857; Baillon, 1874a; Eichler, 1878; Jadin, 1894) indicate that the single symmetry plane of the gynoecium is on the same radius as the first formed sepal (in obliquely abaxial position), which we confirm for *Anacardium* and *Mangifera* L. (see also Jadin, 1894; Wannan, 2006). However, in *Mangifera*, the symmetry plane of the gynoecium is sometimes different from that of the androecium and the flowers may be asymmetric (this study).

Floral isomery and polysymmetry, with three, four or five organs per whorl, is also a common condition in other sapindalean families. In Kirkiaceae, sister to the clade of Anacardiaceae plus Burseraceae (Muellner *et al.*, 2007), the flowers are tetramerous and polysymmetric (Stannard, 1981; Bachelier & Endress, 2008). In Biebersteiniaceae, sister to the remainder of Sapindales (Muellner *et al.*, 2007), the flowers are pentamerous and polysymmetric (Reiche, 1889). In other Sapindales, flowers are also largely isomerous and polysymmetric (Meliaceae, Rutaceae and Simaroubaceae). Largely monosymmetric flowers with oblique monosymmetry are reported in Sapindaceae (Weckerle & Rutishauser, 2003, 2005; Endress & Matthews, 2006b; Ronse de Craene & Haston, 2006).



Calyx and floral cup

Flowers with free and with congenitally united sepals are present in both families (more often united in Burseraceae than in Anacardiaceae). Sepal initiation is spiral, with sepals 1 and 3 in the anterior position, 4 and 5 lateral and 2 posterior (this study; Payer, 1857; Marchand, 1868; Baillon, 1874b; Sattler, 1973). Aestivation is imbricate (quincuncial) or valvate, without postgenital coherence. The first two sepals are often larger than the inner ones. At anthesis, they

Figure 42. Flower buds and anthetic flowers; Anacardiaceae ('male' or 'female' is meant in a functional and not morphological sense). A–C, Spondiadoideae. A, *Solenocarpus philippinensis*, late anthetic flower, lateral view, stamen filaments with anthers fallen, ventral side of the single carpel. B–C, *Campnosperma squamatum*. B, early anthetic male flower, from above, antesepalous stamens longer than antepetalous ones, nectary disc, one carpellode. C, anthetic female flower, from above, nectary disc, one carpel with irregularly lobed stigma. D–L, Anacardioideae. D–E, *Anacardium occidentale*, anthetic flower. D, from above, petals recurved with longitudinal ridges, one stamen much longer than the others, style very long. E, from below, sepal sequence numbered. F–H, *Mangifera indica*. F, late floral bud, from above, corolla contort. G–H, anthetic flower. G, from above, petals with ventral longitudinal ridges, extrastaminal nectary lobes (arrows), single fertile stamen on same radius as carpel. H, from below, sepals and petals reflexed. I, *Blepharocarya involucrigera*, anthetic cupular female inflorescence, lateral view, one half removed, anthetic female flowers densely packed surrounded by fused inflorescence bracts, stigmas small (arrowheads). J, *Schinus molle*, early anthetic female flower, from above, cochlear petal aestivation, sterile stamens, gynoecium trimerous. K, *Semecarpus australiensis*, anthetic male flower, petals with longitudinal ridges, stamens antesepalous. L, *Semecarpus riparius*, anthetic female flower, stamens antesepalous and sterile, gynoecium trimerous. Scale bars, 1 mm.

have an open aestivation distally, whereas at the base their margins may still overlap (if not be united). The free parts of the sepals are often short and commonly obtuse to acute. The sepal margins are more or less fringed in both families, especially towards the tips. If a floral cup is present, it encompasses the bases of the sepals, petals and stamens. However, the sepal margins remain free and are not involved in the floral cup in *Bursera* (Burseraceae) and *Thyrsodium* Salzm. ex Benth. (Anacardioideae) (this study; J. Bachelier, pers. observ.).

In Sapindales, floral cups are also present in Kirkiaceae and Sapindaceae. Free sepal margins on a floral cup and floral base are neither restricted to the clade of Anacardiaceae plus Burseraceae nor to Sapindales, but are also common in other rosids (Matthews *et al.*, 2001; Matthews & Endress, 2002, 2005a, b, 2008; Endress & Matthews, 2006b). In other malvids, a floral cup is present in Brassicales (Bretschneideraceae, Capparaceae, Caricaceae, Moringaceae and Tropaeolaceae) and Huerteales (Tapisciaceae and Gerrardinaceae) and may thus be homoplasious (Alford, 2006; Ronse de Craene & Haston, 2006; Bachelier & Endress, 2008; Worberg *et al.*, 2009).

Sepals commonly have one median and two lateral vascular traces, as in most other rosids. In Burserceae, the lateral bundles commonly form synlaterals in the floral base when they are free or in the synsepalous region when they are united (this study; Marchand, 1868; Lam, 1932a, b; Narayana, 1960a, b). In contrast in Anacardiaceae, synlaterals are more rarely formed (this study). In addition, the lateral traces are often weakly differentiated and only the median trace is sometimes present (*Blepharocarya* and *Campnosperma*). More rarely, there are more than two lateral traces (*Anacardium*).

Corolla

Petal aestivation is more uniform at the familial level in Burseraceae than in Anacardiaceae. In Burseraceae, it is regularly valvate, except for *Commiphora*, in which it is imbricate (sometimes cochlear), whereas in Anacardiaceae it is either valvate or imbricate (quincuncial, contort or cochlear) in pentamerous flowers (this study; Payer, 1857; Baillon, 1874a, b; Leenhouts, 1956; Daly, 1997; Mitchell, 1997). In both families petal aestivation may be shortly open at the base. Postgenital coherence is formed between the petals margins in all aestivation patterns. At anthesis, the petals are commonly free in both families. Petals are acute to acuminate in Burseraceae and Spondiadoideae with valvate tips. The incurved part of the petals in valvate aestivation has large flat margins, whereas, lower down, the margins are more or less oblique to slightly imbricate (this study; Marchand, 1869; Lam, 1932c). The position of the sepal and petal margins may change along their length within a bud, as in *Commiphora* (Burseraceae) and *Buchanania* and *Pseudospondias* Engl. (Spondiadoideae).

A sympetalous corolla is only present in some Protieae (Burseraceae), in *Protium*, *Tetragastris* Gaertn. and *Trattinickia* Willd. (Marchand, 1868; Engler, 1874, 1896; Lam, 1932c; Daly, 1989, 1997). In both families, petals are often longer than sepals in bud and thus protect the inner floral organs when the sepal aestivation becomes open during development (this study; Srinivasachar, 1940). Postgenital coherence is commonly formed between the margins of the petals by interdentation of unicellular and/or short uniseriate multicellular papillae, by striate cuticular ornamentation and maybe by secretion.

In some Anacardiaceae, petals have conspicuous longitudinal ridges on the ventral side, such as in *Anacardium*, *Mangifera* and *Semecarpus* L. f. (Anacardioideae) and *Pleiogynium* Engl. (Spondiadoideae). The epidermis of the ridges is secretory in *Mangifera* and *Anacardium*, but apparently not in *Semecarpus* and *Pleiogynium* (this study). Petals commonly have a single vascular trace, as in most other rosids,

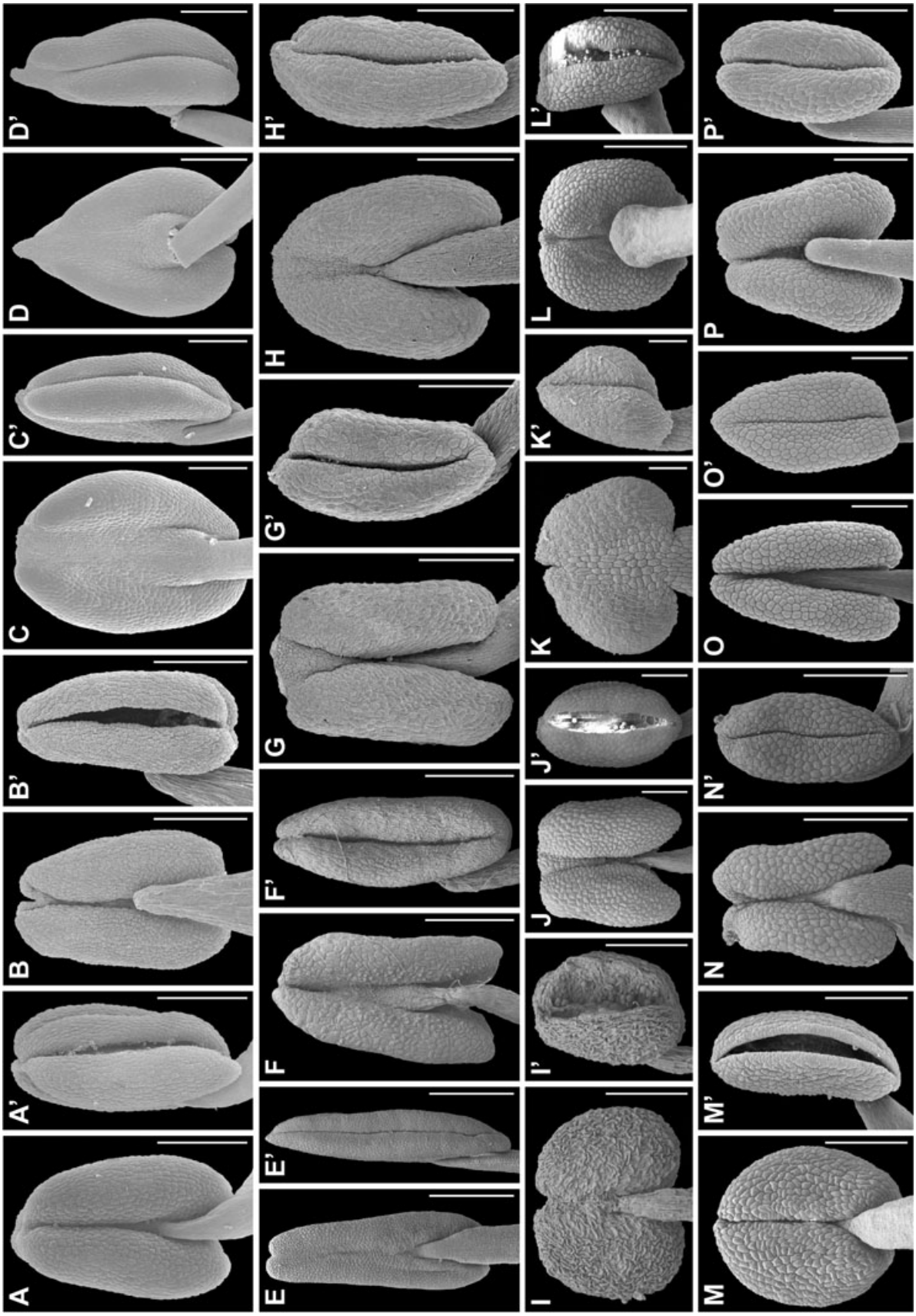

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Figure 43. Anthetic anthers. A–P, dorsal view. A′–P′, lateral view, ventral side at right. A–D, A′–D′, Burseraceae. A–A′, *Beiselia mexicana*, from male flower, antesepalous. B–B′, *Protium obtusifolium*, from male flower, antesepalous. C–D, C′–D′, *Commiphora caudata*, from male flower. C–C′, Antesepalous. D–D′, Antepetalous. E–K, E′–K′, Anacardiaceae, Spondiadoideae. E–E′, *Dracontomelon dao*, from bisexual flower. F–F′, *Spondias dulcis*, from bisexual flower, antesepalous. G–H, G′–H′, *Pleiogynium solandri*, from male flower. G–G′, antesepalous. H–H′, antepetalous. I–I′, *Pseudospondias longifolia*, from male flower, antesepalous. J–J′, *Tapirira* sp., from male flower, antesepalous. K–K′, *Campnosperma squamatum*, from male flower, antesepalous. L–P, L′–P′, Anacardiaceae, Anacardioideae. L–L′, *Anacardium occidentale*, from male flower fertile antesepalous anther. M–M′, *Mangifera indica*, from bisexual flower, fertile antesepalous anther. N–N′, *Blepharocarya involucrigera*, from male flower, antesepalous. O–O′, *Schinus molle*, antesepalous. P–P′, *Semecarpus australiensis*, from male flower, antesepalous. Scale bars, 300 μm (A–H, L–N, P); 100 μm (I–K, O).

although in *Bursera* (Burseraceae) there may be one or two additional, smaller ones.

Sympetaly is also uncommon in other Sapindales. Protection of the inner structures before anthesis by the corolla may be a synapomorphy for Sapindales, lacking in Sapindaceae (for details see Ronse de Craene & Haston, 2006: 468). However, it has also been reported in a number of other rosid groups (e.g. most Celastrales, some Oxalidales, some Crossosomatales, a few Chrysobalanaceae *sensu lato*; Matthews & Endress, 2002, 2005a, b; Endress & Matthews, 2006b; Matthews & Endress, 2008; and part of Fabaceae; Prenner, 2004; Prenner & Klitgaard, 2008). Ventral petal elaborations associated with a nectary are also present in some other malvids (Vogel, 2000; Endress & Matthews, 2006a).

Androecium

The presence of two whorls of stamens is most common in Burseraceae and Anacardiaceae, except for a few haplostemonous genera in Burseraceae and Anacardioideae (see below; Marchand, 1868, 1869; Engler, 1874, 1876, 1892, 1896a; Leenhouts, 1956; Ding Hou, 1978; Daly, 1989; Mitchell & Daly, 1993) and a few other genera with more than two whorls of stamens (see below; Marchand, 1869; Engler, 1876, 1892; Lam, 1932b; Ding Hou, 1978; von Teichman & Robbertse, 1986; Breteler, 2003). Flowers with two stamen whorls are commonly obdiplostemonous (because they have antepetalous carpels) in both families, except for Anacardioideae (Baillon, 1874a; Engler, 1896, 1931a; Lam, 1932b; Narayana, 1960a, b).

Development of the two-whorled androecium is similar in both families. In early stages, the antepetalous stamens are often shorter and/or narrower/thinner than the antesepalous ones or are as developed as the antesepalous ones. At anthesis, they remain shorter or are equally developed (this study; Baillon, 1874a; Leenhouts, 1956; Daly, 1989). Rarely in Burseraceae (some *Protium* species), the antepetalous stamens become even slightly longer (this study; Daly, 1992). In both families, the antepetalous anthers also tend to be more apiculate (this study).

In haplostemonous flowers, only antesepalous stamens are present in Burseraceae, such as in *Triomma*, some species of *Canarium* L. and *Santiria* Blume and in male flowers of *Crepidospermum* Hook. f. and in Anacardioideae (Marchand, 1868, 1869; Engler, 1874, 1876; Ding Hou, 1978; Mitchell & Daly, 1993). This condition may be interpreted as loss of the antepetalous stamen whorl. Stamens are commonly free in both families, but, in some Canarieae (Burseraceae) and Anacardioideae with two stamen whorls, the filament bases are united and form a tube around the gynoecium. In Anacardioideae, the androecium is rarely monosymmetric by the extreme development of a single stamen, as in *Anacardium* and *Mangifera* (this study; Copeland, 1961) and may even be reduced to a single stamen as in *Fegimanra* Pierre (Engler, 1897; Mitchell, 1997). In a few other genera, more than two whorls of stamens are present: in Burseraceae in some *Canarium* (Lam, 1932b) and in Anacardiaceae in *Sclerocarya* Hochst. (Spondiadoideae; von Teichman & Robbertse, 1986) and *Gluta* L. and *Sorindeia* Thouars (Anacardioideae; Ding Hou, 1978; Breteler, 2003).

Stamen structure is similar in the two families (especially Burseraceae and Spondiadoideae) (Figs 43, 44). There are two extreme types of stamen shape with a range of intermediate conditions in both families. In type 1, the anther tends to be shorter than the filament, versatile, caducous and (almost) latrorse (or slightly introrse). The filament tip is constricted and the transition zone from filament to anther extends shortly into a narrow and thin connective (Fig. 44C, D, L, M). In type 2, the filament tends to be shorter and stouter than in type 1, the anther tends to be longer than the filament and is markedly introrse (Fig. 44E–G). The attachment is not constricted and the transition zone from filament to anther extends into a thicker and broader connective. Such anthers tend to be apiculate. Type 1 is most frequently observed in Spondiadoideae (and some Burseraceae: *Beiselia*, *Bursera* and *Protium*), but in core Burseraceae, especially in Canarieae, type 2 is more frequent. In Anacardioideae, stamen structure is commonly intermediate between the two types. An apical beak is

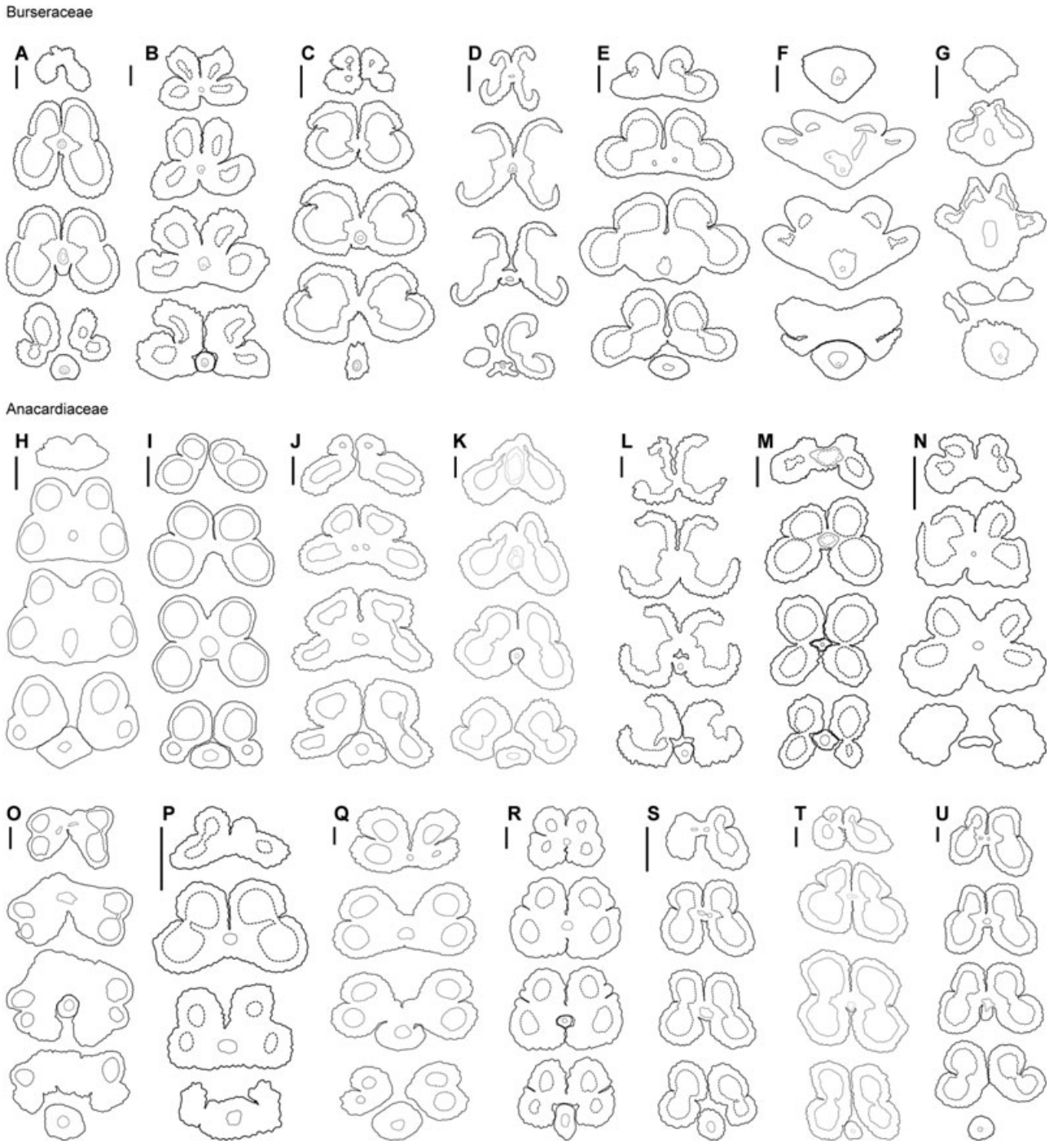

Figure 44. Anthetic anthers. Transverse section series from top, downwards. Morphological surfaces drawn with thick continuous lines; pollen sacs shown with thick broken lines; vascular bundles drawn with thin continuous lines and associated resin canals with thin broken lines. A–G, Burseraceae. A, *Beiselia mexicana*. B, *Protium morii*. C, *Protium obtusifolium*. D, *Bursera* sp. E, *Commiphora caudata*. F, *Canarium caudatum*. G, *Santiria* cf. *apiculata*. H–P, Anacardiaceae. Spondiadoideae. H, *Dracontomelon dao*. I, *Spondias dulcis*. J, *Spondias purpurea*. K, *Pleiogynium solandri*. L, *Pseudospondias longifolia*. M, *Tapirira* sp. N, *Buchanania arborescens*. O, *Solenocarpus philippinensis*. P, *Campnosperma squamatum*. Q–U, Anacardiaceae, Anacardioideae. Q, *Anacardium occidentale*. R, *Mangifera indica*. S, *Blepharocarya involucrigera*. T, *Schinus molle*. U, *Semecarpus australiensis*. Scale bars, 100 μm.

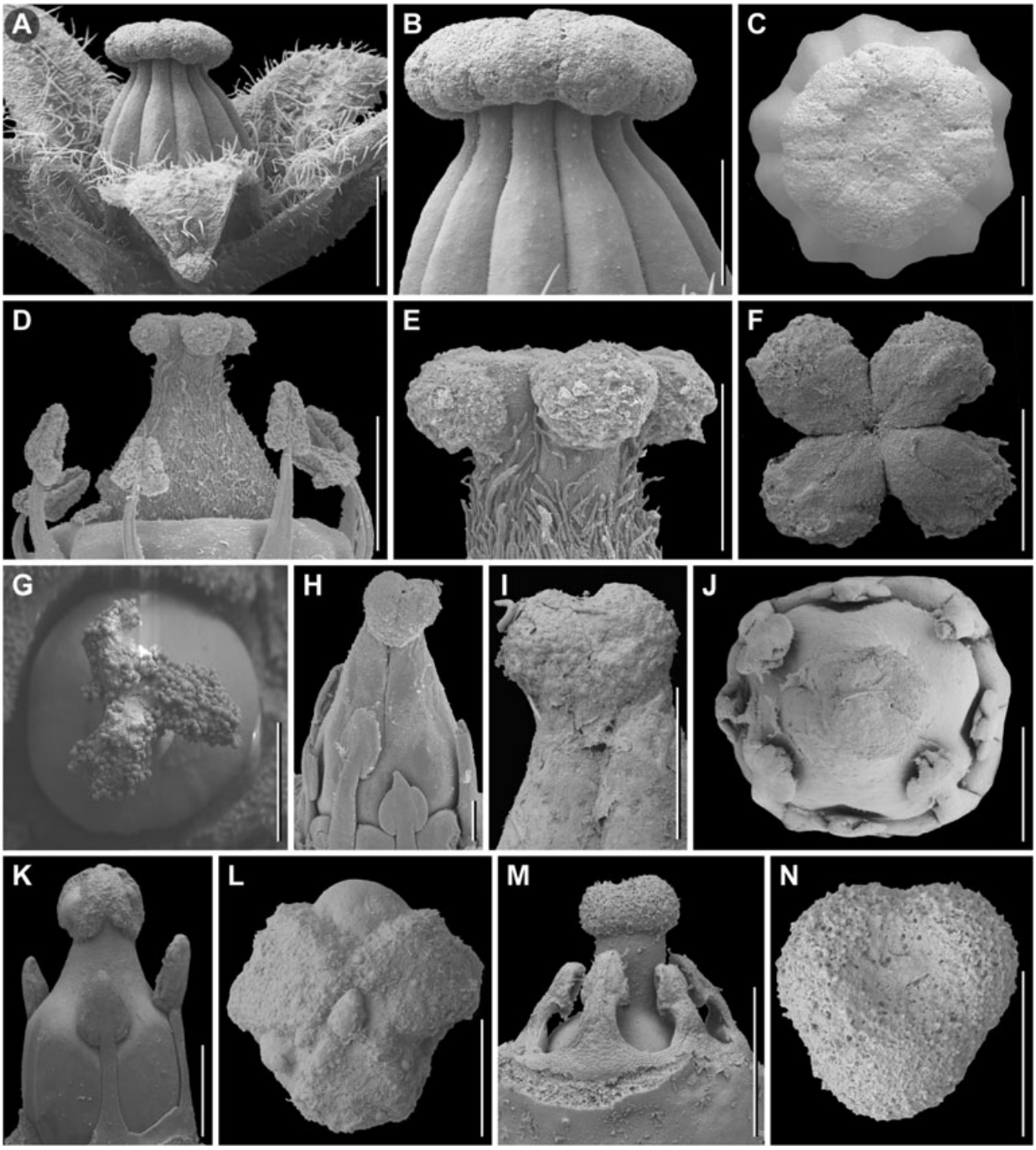

Figure 45. Anthetic gynoecium. Burseraceae. A–C, *Beiselia mexicana*, from female flower. A, lateral view, gynoecium with longitudinal furrows between the carpels. B–C, stigmatic head of ten carpels with secretion. B, lateral view. C, from above. D–F, *Protium morii*, from female flower. D, lateral view, petals removed. E–F, stigmatic head of four carpels with secretion. E, lateral view. F, from above, carpel tips reflexed with ventral longitudinal slits. G, *Bursera* sp., from bisexual flower, from above, stigmatic head of three carpels with secretion and pollen grains. H–J, *Commiphora caudata*, from female flower. H, lateral view, perianth removed, nectary lobes between staminodes appressed to gynoecium, longitudinal furrow between the two carpels. I, close-up, other side of stigmatic head with secretion. J, from above. K, L, *Canarium caudatum*, from female flower. K, lateral view, perianth removed, nectary lobes between sterile stamens appressed to gynoecium. L, from above, stigmatic head of three carpels with secretion. M–N, *Santiria* cf. *apiculata*, from female flower. M, lateral view, perianth removed, staminodes united around the gynoecium. N, from above, close-up, stigmatic head of three carpels with secretion. Scale bars, 1 mm (A, D, K); 500 μm (B–C, E–F, J, L–M); 250 μm (G–I, N).

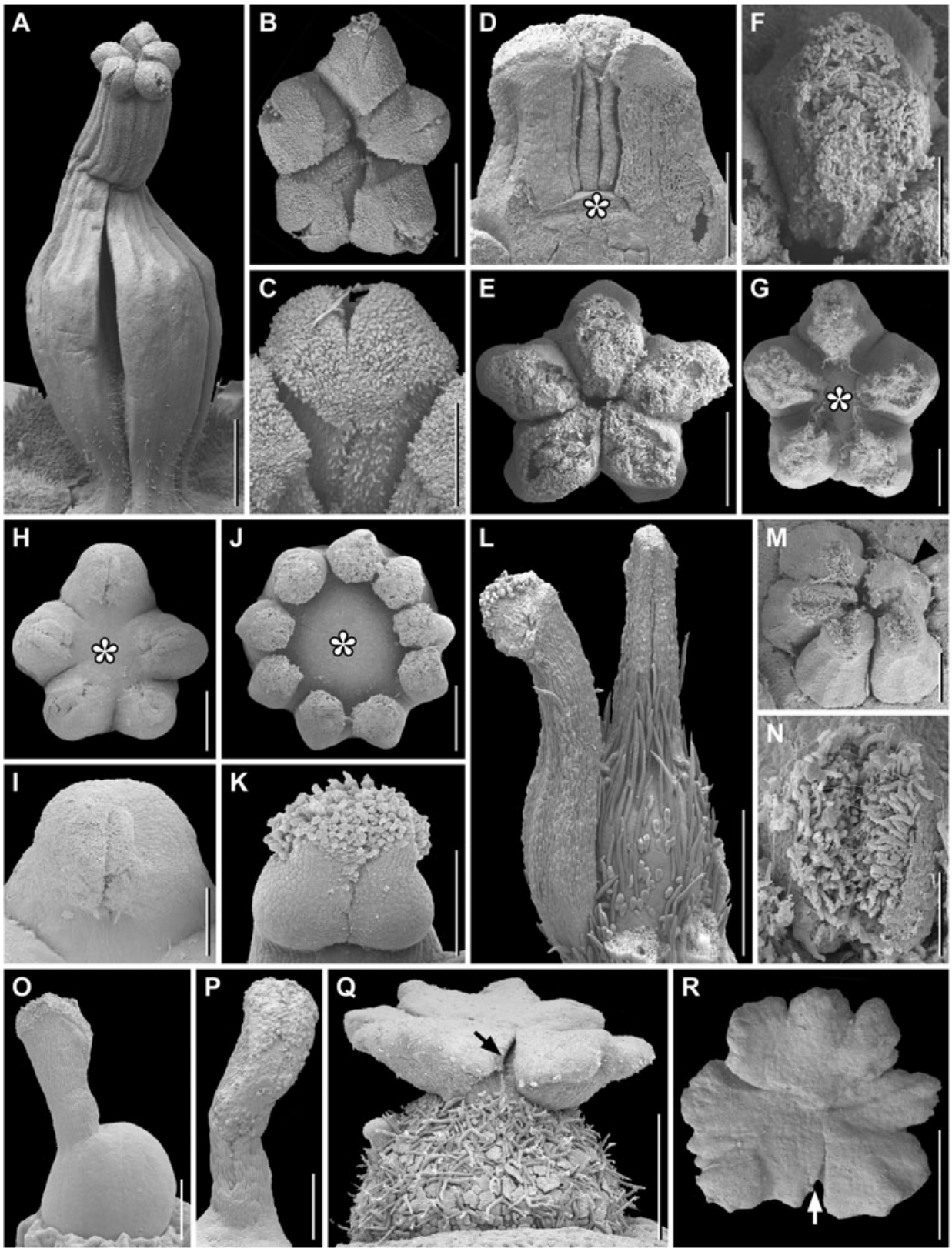
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Figure 46. Anthetic gynoecium (G postanthetic). Anacardiaceae, Spondiadoideae. A–C, *Dracontomelon dao*, from female flower. Lateral view, perianth removed, hairs on the flat nectary disk, gynophore and carpel bases, gynoecium with longitudinal furrows between the carpels. B, from above, stigmatic head of five carpels, each ending in a slit-shaped stigma (some with pollen grains). C, close-up of a stigma. D–G, *Spondias dulcis*, from female flower. D, lateral view, three contiguous styles (two carpels removed), former floral apex hidden (asterisk). E, from above. F, close-up, papillate stigma with secretion. G, from above, stigmas moved outwards, former floral apex exposed (asterisk). H–I, *Spondias purpurea*, from female flower. H, from above, gynoecium with five free short styles and stigmas, former floral apex exposed (asterisk). I, close-up, style with ventral longitudinal slit, stigma with secretion. J–K, *Pleiogynium solandri*, from female flower. J, from above, gynoecium with nine free short styles and stigmas, some adjacent stigmas contiguous, former floral apex exposed (asterisk). K, close-up, style with ventral longitudinal slit, papillate stigma with secretion. L–N, *Buchanania arborescens*, from female flower. L, lateral view, two sterile carpels removed, fertile carpel at rigth, one sterile carpel at left. M, five carpels, fertile carpel indicated by arrowhead. N, close-up, papillate stigma of a sterile carpel, covered with secretion and pollen grains. O–P, *Solenocarpus philippinensis*, from bisexual or female flower, unicarpellate gynoecium. O, lateral view, carpel with ventral side at right. P, close-up, stigma and style with ventral slit, stigma papillate with secretion and pollen grains. Q–R, *Campnosperma squamatum*, from female flower, unicarpellate gynoecium. Q, lateral view, peltate and stellate hairs on ovary, irregularly lobed discoid stigma with deep ventral slit (arrow). R, from above, flattened stigma with secretion (arrow points to ventral slit). Scale bars, 1 mm (A); 500 μm (B, E, G–H, J, L, Q–R); 250 μm (C–D, F, I, K, M, O–P); 100 μm (N).

sometimes present in both families, more or less curved to the ventral side of the anthers, such as *Canarium* in Burseraceae, *Pleiogynium* (antepetalous stamens) and *Tapirira* Aubl. in Spondiadoideae and *Pistacia* in Anacardioideae.

In both families, anthers tend to have a papillate surface with conspicuous striate cuticular ornamentations (Fig. 43) (this study; Narayana, 1960b). There is a single vascular bundle in each stamen, as in most other rosids, and it sometimes branches in the anthers in both families (this study), in *Canarium* and *Commiphora* (Burseraceae), in *Solenocarpus* Wight & Arn. and *Spondias* (Spondiadoideae) and in *Blepharocarya* and *Semecarpus* (Anacardioideae).

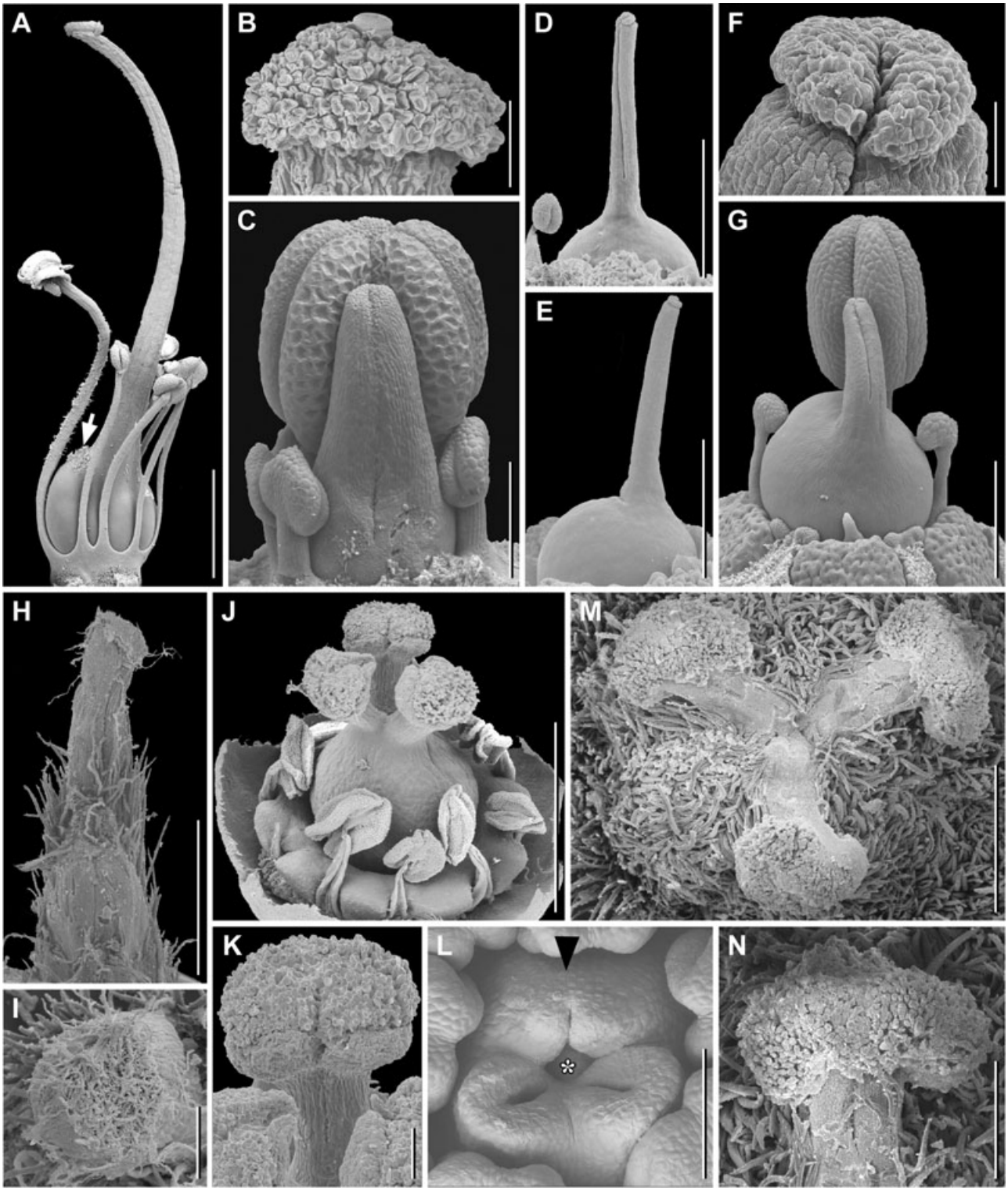
In other Sapindales, isomerous, obdiplostemonous flowers as in Anacardiaceae and Burseraceae are present in Meliaceae *p.p.* (Harms, 1940), Rutaceae (Beille, 1902; Engler, 1931b; Eckert, 1966; Gut, 1966) and Simaroubaceae (Baillon, 1874a; Engler, 1931c; Nair & Joseph, 1957; Nair & Joshi, 1958; Narayana & Sayeeduddin, 1958; Eckert, 1966). Haplostemonous flowers with the stamens antesepalous as in some Anacardioideae and Burseraceae are present in Kirkiaceae (Bachelier & Endress, 2008), Meliaceae (Harms, 1940), Rutaceae (Beille, 1902; Engler, 1931b; Eckert, 1966; Gut, 1966) and Simaroubaceae (Engler, 1931c; Nair & Joshi, 1958; Nair & Sukumaran, 1960).

Both kinds of stamen shape are also common in other Sapindales and other rosids with sagittate, basifixed to dorsifixed anthers with slightly latrorse to introrse, longitudinal dehiscence slits, which extend (almost) along the entire length of the thecae (Endress & Stumpf, 1991; Matthews & Endress, 2002, 2004, 2005a, b, 2006; Bachelier & Endress, 2007, 2008; Matthews & Endress, 2008). In Burseraceae and Anacardiaceae, the dorsal side of the thecae is slightly curved backwards at the zone of transition from filament to anther but commonly does not form a distinctive pseudopit. In contrast, a distinctive pseudopit occurs in other Sapindales, e.g. *Kirkia* (Kirkiaceae; Bachelier & Endress, 2008), *Ailanthus* Desf. (Simaroubaceae), *Acer p.p.*, *Aesculus* L., *Koelreuteria* Laxm., and *Xanthoceras* Bunge (Sapindaceae), *Melia* (Meliaceae), *Correa* Andrews, *Pilocarpus* Vahl. and *Ptelea* L. (Rutaceae) (see Endress & Stumpf, 1991).

Nectary disc

A conspicuous nectary disc (or nectary lobes) is usually present in Anacardiaceae and Burseraceae. It is intrastaminal, except for *Mangifera* (Anacardioideae) (Copeland, 1961; Mitchell, 1997) and *Triomma* (Burseraceae) (Leenhouts, 1956). The surface of the nectary is often glabrous, smooth to papillate and contains nectar pores. Sometimes, it is also covered with hairs, as in *Semecarpus*.

The development of the nectary disc between the stamen and gynoecium bases appears to be affected by the presence of a floral cup and, in addition, its expansion within the cup appears to be limited by that of a fertile gynoecium (in functionally female flowers). As a result, it is often reduced to flattened or cushion-like lobes, which expand more or less between the filament bases, as in *Commiphora* (Burseraceae). In functionally male flowers of some Burseraceae, the nectary disc may encompass the reduced gynoecium and they may jointly form a conical structure called an 'ovariodisk' by Lam (1932c) (see also Engler, 1896; Leenhouts, 1956; Daly, 1989). The conical structure in the centre of the male flower of



Beiselia may also be seen as a reduced 'ovariodisk'. The disc also encompasses the base of the ovary wall in *Semecarpus* (Anacardioideae, this study). In *Mangifera* (Anacardioideae), the nectary is either restricted to dorsal pads at the base of the filaments or completely encompasses the filament bases (this study; Copeland, 1961; Mitchell, 1997). Nectary disc or lobes are lacking in the wind-pollinated *Campylo-*

Figure 47. Anthetic gynoecium [(C, G, L) from bud]. Anacardiaceae, Anacardioideae. A–C, *Anacardium occidentale*. A–B, from female flower, unicarpellate gynoecium. A, lateral view, perianth removed, united stamen bases around gynoecium, carpel ventral side at right, hairs on ovary dorsal side indicated by arrow. B, close-up, dry papillate stigma. C, ventral side of carpel, fertile stamen behind carpel more developed than other stamens. D–G, *Mangifera indica*. D–F, from female flower, unicarpellate gynoecium, lateral view. D, ventral side of carpel (with ventral slit) ending in short stigma. E, ventral side of carpel at left. F, close-up, dry papillate stigma. G, ventral side of carpel, with the single fertile stamen behind but on a different radius and small staminodes. H–I, *Blepharocarya involucrigera*, from female flower. H, lateral view, perianth removed, carpel ventral side with longitudinal slit, ending in a short stigma. I, from above, close-up, papillate stigma with secretion. J–L, *Schinus molle*. J–K, from female flower. J, perianth removed, trimerous gynoecium with three stigmatic branches. K, close-up, stigmatic branch ventral side with longitudinal slit, ending in a papillate stigma with secretion. L, from above, fertile carpel indicated with arrowhead and former centre of the floral apex indicated with asterisk. M–N, *Semecarpus riparius*, from female flower, trimerous gynoecium. M, from above, three stigmatic branches. N, close-up, stigmatic branch ventral side with longitudinal slit, papillate stigma with secretion. Scale bars, 1 mm (A, D, E); 50 μm (B, F); 200 μm (C); 500 μm (G–H, J, M–N); 100 μm (I, K–L).

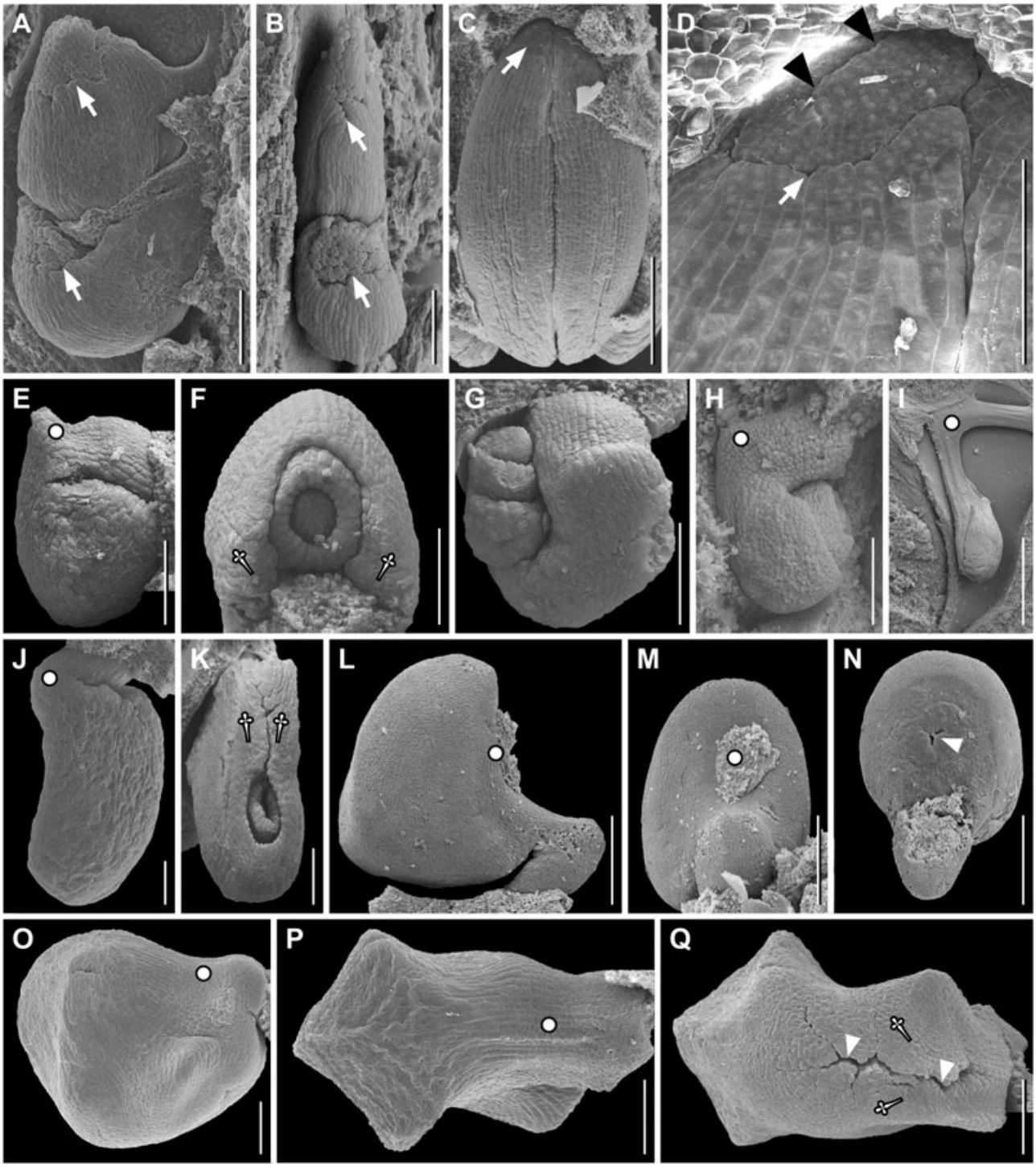
petalum Forman (Forman, 1954), *Amphipterygium* and *Pistacia* (Bachelier & Endress, 2007). The nectary disc is also lacking in *Anacardium* (Copeland, 1961), but nectar is produced by secretory hairs (glands) with unicellular or uniseriate bicellular stalks and multicellular heads, clustered mostly between the petal and united stamen bases (Moncur & Wait, 1986; Moncur, 1988; Wunnachit *et al.*, 1992).

An intrastaminal nectary disc is also common in other Sapindales such as Kirkiaceae, Rutaceae, Meliaceae and Simaroubaceae; in Sapindaceae, it is intra- and extrastaminal (Ramp, 1988; Ronse de Craene & Haston, 2006; Bachelier & Endress, 2008). An intrastaminal disc is also common in other malvids and an extrastaminal nectary disc has been interpreted as a derived condition (Ronse de Craene & Haston, 2006).

Gynoecium

The gynoecium is syncarpous in both families. Even in *Buchanania*, in which the unusual gynoecium has been described as either completely apocarpous (Marchand, 1869; Baillon, 1874a; Engler, 1876, 1892; Wannan, 2006) or basally syncarpous (Wannan & Quinn, 1991), our results show the presence of a short syncarpous zone. Our findings are in line with Robbertse, von Teichman & van Rensburg (1986), who noted that completely apocarpous gynoecia may not be present in Anacardiaceae. In both families, the gynoecium commonly comprises between five and two carpels. There is a trend towards reduction of carpel number, probably starting from an isomerous state. The reverse, presence of more than five carpels in a whorl also occurs in both families but is rarer (this study; Baillon, 1874a; Wannan & Quinn, 1991; Wannan, 2006). In *Beiselia* (Burseraceae) and *Pleiogynium* (Spondiadoideae), up to 12 carpels are present. Only in Anacardiaceae are there two prominent features of gynoecium reduction: (1) unicarpellate (monomerous) gynoecia are scattered in each subfamily, for example, *Campnosperma* and *Solenocarpus* in Spondiadoideae and *Anacardium*, *Blepharocarya* and *Mangifera* in Anacardioideae (this study; Marchand, 1869; Wannan & Quinn, 1991); (2) more importantly, there is a trend of reduction in number of fertile carpels by unequal development. The gynoecium then comprises fewer locules than there are carpels, but there are either still more than one in some Spondiadoideae (e.g. sometimes in *Harpephyllum* Bernh. ex Krauss, *Lannea* A. Rich. and *Sclerocarya*) or the syncarpous ovary is unilocular and pseudomonomerous (e.g. in *Tapirira* and *Harpephyllum*) (this study; Marchand, 1869; Kelkar, 1958a; von Teichman & Robbertse, 1986; von Teichman, 1988a; von Teichman & van Wyk, 1988; Wannan & Quinn, 1991). In Anacardioideae, it is (pseudo)monomerous (with two of the three carpels reduced) (this study; Payer, 1857; Marchand, 1869; Baillon, 1874a; Copeland, 1959; Wannan & Quinn, 1991; Gallant, Kemp & Lacroix, 1998; Bachelier & Endress, 2007).

In Burseraceae, the gynoecium is synascidiate at least up to the midpoint of the ovary and symplicate up to the base of the free stigmas. However, in contrast to core Burseraceae, in *Beiselia* the synascidiate region encompasses the whole ovary and extends beyond the locules and the symplicate zone below the postgenitally united free carpel tips is short. In Spondiadoideae with a plurilocular gynoecium, the synascidiate zone also extends beyond the locules, but a symplicate zone is totally lacking. The former centre of the floral apex is thus enclosed in the ovary in core Burseraceae. In contrast in *Beiselia* and (multicarpellate) Spondiadoideae, the former centre of the floral apex is uplifted to the base of the free carpel tips and it is therefore either exposed at anthesis, as in *Spondias purpurea* or *Pleiogynium* (Spondiadoideae), or hidden between the connivent (*S. dulcis*) or postgenitally united free carpel tips (*Beiselia* and *Dracontomelon* Blume) (for style position in Spondiadoideae, see also Mitchell *et al.* (2006). This development of



the former centre of the floral apex, shared by representatives of both families, is an otherwise rare feature.

In the pseudomonomerous gynoecium of most Anacardioideae and some Spondiadoideae, the unequal development of the three carpels (sometimes more in Spondiadoideae) and the various degrees of reduction of the sterile carpels make it sometimes difficult (if not impossible) to use the terminology of Leinfellner (1950), traditionally used to describe a syncarpous gynoecium, as noted by Bachelier & Endress (2007). In Anacardiaceae, there is a correlation between the development of the synascidiate zone and the insertion level of the ovule in the locule (the more devel-

Figure 48. Anthetic ovules. A–D, Burseraceae. Border between outer and inner integument indicated by arrows. A, B, *Beiselia mexicana*, A, lateral view, placentae at right, two superposed ovules, micropyles directed upwards. B, frontal view. C–D, *Canarium caudatum*. C, lateral view, two collateral ovules, micropyles directed upwards. D, close-up, slit-shaped micropyle (arrowheads). E–K, Anacardiaceae, Spondiadoideae. E–G, *Dracontomelon dao*. E, lateral view, placenta at right, region of the *ponticulus* marked with circle. F, frontal view, micropyle open, inner integument longer than the hood-shaped outer integument, which develops two lateral flaps (flap initials marked with crosses). G, atypical situation, with an additional, smaller, antitropous ovule (at left). H–I, *Spondias dulcis*, lateral view, placenta at right, region of the *ponticulus* marked with circle. H, at anthesis. I, after anthesis. J–K, *Pleiogynium solandri*. J, lateral view, placenta at right, region of the *ponticulus* marked with circle. K, frontal view, inner integument forming slit-shaped endostome, outer integument hood-shaped with two lateral flaps marked with crosses. L–Q, Anacardiaceae, Anacardioideae. L–N, *Anacardium occidentale*. L, lateral view, placenta at base, region of the *ponticulus* marked with circle. M, view from side of *ponticulus*, region of *ponticulus* marked with circle. N, frontal view, with micropyle (arrowhead). O–Q, *Schinus molle*. O–P, lateral view, placenta at right, region of the *ponticulus* marked with circle. P, view from side of *ponticulus*, region of the *ponticulus* marked with circle Q, from below, micropyle (arrowheads), slit-shaped, irregularly lobed, formed by the outer integument, two large lateral flaps marked with crosses. Scale bars, 100 μm (A–B, D–K, O–Q); 300 μm (C, L–N).

oped, the higher) (Robbertse *et al.*, 1986). Therefore, a basal insertion of the funicle–ovule complex, as in *Buchanania* (Spondiadoideae) and *Anacardium* and *Mangifera* (Anacardioideae), would indicate that the former centre of the floral apex was not uplifted, either because the synascidiate region is unusually weakly developed (*Buchanania*) or because the gynoecium is truly monomerous, not pseudomonomerous (*Anacardium* and *Mangifera*). An apical or subapical insertion of the median ovule would indicate that the former centre of the floral apex was uplifted along the ventral side of the fertile carpel, with the entire sterile carpels (*Blepharocarya*, *Semecarpus* and *Schinus*).

The single locule of the syncarpous gynoecium thus appears 'ascidiate', but the ovary wall also comprises the solid bases of the reduced carpels (see Eckardt, 1937; Bachelier & Endress, 2007). Interpretation of a gynoecium as monomerous or pseudomonomerous is not always easy if the reduction is far advanced (Eckardt, 1937; Müller-Doblies, 1970; Bachelier & Endress, 2007). Some genera, especially *Anacardium* and *Mangifera* (Anacardieae), are sometimes interpreted as pseudomonomerous with two carpels reduced (Copeland, 1961; Wannan & Quinn, 1991). Mango 'Hadden' and 'Sensation' can have more than one carpel, which are congenitally united at the base but free for most of their length (Robbertse *et al.*, 1986). If *Anacardium* and *Mangifera* were pseudomonomerous, the remnants of the two reduced carpels would be expected either at the base of the ventral slit of the fertile carpel or united with the fertile carpel along the two flanks of the ventral slit up to the stigma. As yet, convincing evidence for either configuration is lacking, but pseudomonomery cannot be excluded. A gynophore is only present in some Anacardiaceae (Engler, 1892), such as *Dracontomelon* in Spondiadoideae (this study) and *Gluta* in Anacardioideae (Ding Hou, 1978).

A stigmatic head formed by the postgenital union of the free stigmas and distal part of the styles above the syncarpous zone is present in both families, but is common in Burseraceae and rare in Anacardiaceae, in which it occurs in *Dracontomelon* (Spondiadoideae) and sometimes partially in *Pleiogynium*. In all these cases of postgenital union, a complete or incomplete external compitum appears to be present. In some Protieae (Burseraceae) and *Dracontomelon* (Spondiadoideae), the tips of the carpels are free and reflexed beyond the zone of postgenital union of the stigmatic head.

The stigmas usually have uniseriate, multicellular papillae with two to five cells; more rarely these are unicellular (this study). The multicellular papillae tend to be densely packed and may wrongly appear unicellular. In *Campylopetalum* (under Podoaceae) and *Cotinus* Mill. (Anacardioideae), stigmas were described as non-papillate by Heslop-Harrison & Shivanna (1977). However, we found a papillate stigma in *Cotinus*. The stigmas are commonly wet at anthesis in both families, but secretion is often more conspicuous in Burseraceae than in Anacardiaceae and can massively cover the stigmatic head (this study; Sunnichan, Mohan Ram & Shivanna, 2005). Only in Anacardioideae does the stigma sometimes appear to be dry at anthesis, as in *Anacardium* and *Mangifera* (former Anacardieae; this study), and *Campylopetalum* (under Podoaceae) (Heslop-Harrison & Shivanna, 1977). Presence of secretion may vary as in *Pistacia*, in which it is only released once the stigmas have been in contact with pollen (Martínez-Pallé & Herrero, 1995; Shuraki & Sedgley, 1997).

The PTTTs differentiate along the inner morphological surface of each carpel and are restricted to the inner angle of the ventral slit below the stigmas in both families. Formation of an intragynoecial compitum in a syncarpous gynoecium is based on the presence of a symplicate zone (Endress, Jenny & Fallen,

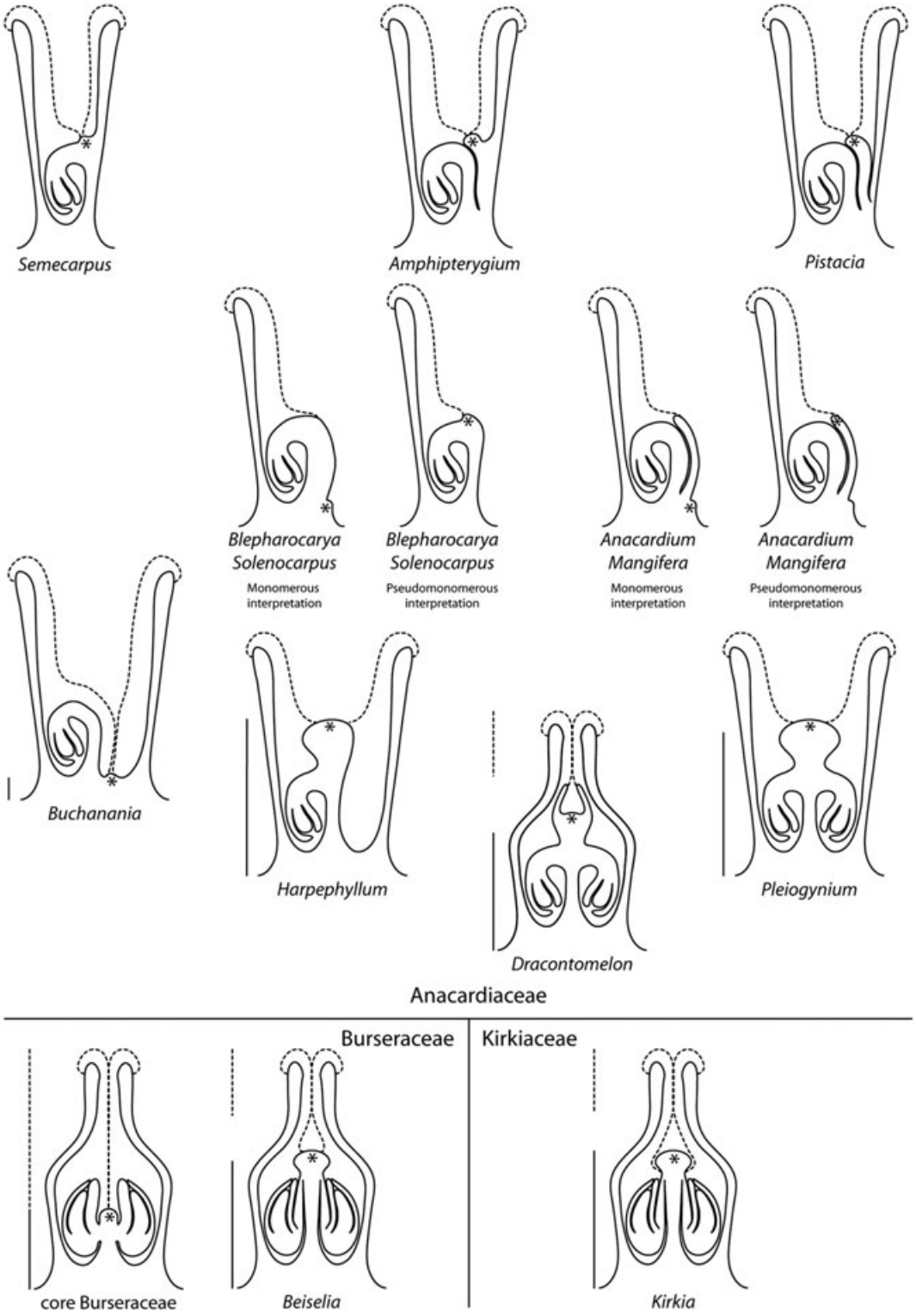


Figure 49. Summary gynoecium structure and diversity in Anacardiaceae, Burseraceae and Kirkiaceae. Schematic median longitudinal section of gynoecium. Parts outside of median plane drawn with broken line. Position of the former centre of the floral apex indicated by asterisk (*Amphipterygium* and *Pistacia* based on Bachelier & Endress, 2007); *Kirkia* based on Bachelier & Endress (2008). On the left side of gynoecia with more than one carpel of about the same length, the extent of the synascidiate zone is marked with a continuous vertical line and the extent of the postgenitally united part of the apocarpous zone with a broken vertical line.

1983; Endress, 1994). Although a symplicate zone is common in Burseraceae, and perhaps some Anacardioideae (e.g. *Pistacia*, *Schinus* and *Semecarpus*), an intragynoecial compitum often does not appear to be present (this study; Bachelier & Endress, 2007). In the unusal gynoecium of *Buchanania*, in which well-developed stigmas and PTTTs are present in the sterile carpels but not in the single fertile carpel, a distinct compitum is lacking. It remains to be studied whether the pollen tubes reach the ovule via undifferentiated tissue in the gynoecium base or whether the plants are apomictic.

In both families, carpels are of angiospermy type 4 (for term, see Endress & Igersheim, 2000). In some Burseraceae, the flanks of the carpels are sometimes not entirely postgenitally fused and may form a hollow stylar canal in the inner angle of the ventral slit. The carpels are then intermediate between types 3 and 4 (*Beiselia* and *Canarium*); sometimes there is a combination of both types within a gynoecium. It is unclear whether the hollow canal and/or the loose slit are filled with secretion. In *Boswellia*, secretion is present along the loose inner angle of the ventral slit (Sunnichan *et al.*, 2005).

In Sapindales in general, the gynoecium is commonly syncarpous. Apocarpous gynoecia are restricted to Simaroubaceae (Narayana, 1957; Nair & Joshi, 1958; Narayana & Sayeeduddin, 1958; Ramp, 1988) and Rutoideae Arn. of Rutaceae (Gut, 1966; Ramp, 1988). Pseudomonomerous gynoecia, to our knowledge, are not reported in any sapindalean family other than Anacardiaceae (*Leitneria* in Simaroubaceae and *Empleuridium* Sond. & Harv. and *Cneoridium* Hook. f. in Rutaceae are supposedly truly monomerous; Pfeiffer, 1912; Engler, 1931b). In contrast, an increase in carpel number occurs in several families (Endress & Matthews, 2006b), such as Kirkiaceae (*Pleiokirkia* Capuron, Capuron, 1961), Sapindaceae (*Distichostemon* F. Muell., Reynolds, 1985), Meliaceae (*Turraea* L., up to 20; Wiger, 1935; Harms, 1940), Rutaceae (*Aegle* Corrêa, up to 20; Vasil & Johri, 1964) and in *Landeenia* Manchester & Hermsen, a fossil related to Sapindales (Manchester & Hermsen, 2000). Apart from Anacardiaceae and Burseraceae (*Beiselia*), a long synascidiate zone with an extensive uplifting of the former centre of the floral apex above the ovary is otherwise only known from Kirkiaceae in Sapindales (Bachelier & Endress, 2008). It may thus be a synapomorphy for the clade of Kirkiaceae and Anacardiaceae plus Burseraceae (Bachelier & Endress, 2008). In other malvids, increase in carpel number and concomitant increase of the remaining floral apex is also present in Gyrostemonaceae and Capparaceae (Brassicales) and Malvaceae (Malvales) (Hufford, 1996; Endress, 2006; Endress & Matthews, 2006b). The development of a gynophore is common in Sapindales and is also widespread in malvids (Endress & Matthews, 2006b).

The presence of a stigmatic head formed by the postgenitally united free carpel tips is a widespread feature in Sapindales (Endress & Matthews, 2006b). It occurs in Kirkiaceae (Bachelier & Endress, 2008), Nitrariaceae (Ronse de Craene & Smets, 1991), Meliaceae (Gouvêa *et al.*, 2008a, b), Rutaceae (Rutoideae) and Simaroubaceae (Endress *et al.*, 1983; Ramp, 1988). The role of the stigmatic head in the formation of an external compitum has only been studied in some Rutaceae among Sapindales (Ramp, 1988). A papillate stigmatic surface is common in Sapindales and also present in all other families, including Meliaceae (Gouvêa *et al.*, 2008a, b), Rutaceae and Simaroubaceae (Ramp, 1988), Sapindaceae (Weckerle & Rutishauser, 2003, 2005) and Nitrariaceae (Ronse de Craene & Smets, 1991), but in most cases it is unknown whether the papillae are uni- or multicellular. Stigmas with uniseriate, multicellular papillae as in Burseraceae and Anacardiaceae are rare in angiosperms and occur elsewhere in Sapindales only in *Kirkia* (Kirkiaceae) (Bachelier & Endress, 2008). However, uniseriate multicellular papillae may be more widespread than previously recorded, as suggested by the contradictory observations of non-papillate vs. papillate stigmas in Rutaceae and Simaroubaceae by Heslop-Harrison & Shivanna (1977) and Ramp (1988).

Ovules

In Burseraceae each carpel has two collateral antitropous ovules, whereas in Anacardiaceae there is a single median syntropous ovule. This distinction is supported in the present study. The ovules are anatropous or campylotropous in both families, and they seem to be more often campylotropous at anthesis in Burseraceae than in Anacardiaceae, where they may become slightly campylotropous later during seed development (as suggested by illustrations in von Teichman, 1993; von Teichman & van Wyk, 1996; Carmello-Guerreiro & Sartori Paoli, 2005; see also Endress & Matthews, 2006b).

Ovules are crassinucellar and commonly bitegmic in both families. Unitegmic ovules also occur in both families but are rare: they occur in a few genera in Anacardioideae (*Amphipterygium*, *Anacardium*, *Lithraea*, *Semecarpus p.p.* and *Mangifera*, this study; Boodle in Hemsley, 1907; Copeland, 1961; Joel & Eisenstein, 1980; Moncur & Wait, 1986; de Wet, Robbertse & Coetzer, 1986; Carmello-Guerreiro & Sartori Paoli, 2005; Bachelier & Endress, 2007) and only a few species in Burseraceae (species of *Canarium*, *Commiphora* and *Santiria*; this study; Wiger, 1935). In *Commiphora* (Burseraceae), the seemingly unitegmic ovule has an outer envelope

well developed on the concave side of the ovule, which may be interpreted as a partial outer integument, and the ovule is thus bitegmic (this study; Shukla, 1954). In Anacardiaceae, unitegmy was tentatively described as fusion of the two integuments in *Anacardium* (Copeland, 1961; Moncur & Wait, 1986), *Mangifera* (Joel & Eisenstein, 1980; de Wet *et al.*, 1986) and *Pistacia* (Marchand, 1869; Copeland, 1955; Shuraki & Sedgley, 1997), as integumentary shifting in *Mangifera* (Robbertse *et al.*, 1986) or as integument splitting in *Pistacia* (of an unitegmic condition originally derived from an ancestral fusion; Grundwag, 1976) and *Lannea* and *Rhus* L. (Kelkar, 1958a, b). In Burseraceae, unitegmy was also tentatively interpreted as fusion of the integuments (Narayana, 1960b). These explanations are vague and it is to be hoped that developmental genetic studies could help to reach an answer, as in the similarly diverse genus *Impatiens* L., in which it has been shown that the unitegmic condition may be reached via different pathways (McAbee, Kuzoff & Gasser, 2005). Lobation of integuments was not studied in detail but some genera of both families have conspicuously lobed outer or single integuments (e.g. *Canarium* and *Commiphora*, Burseraceae; *Anacardium*, Anacardioideae).

In bitegmic ovules, the inner integument is often longer than the outer one and forms the micropyle, which at anthesis is closed in Burseraceae but not always in Anacardiaceae (this study; Bachelier & Endress, 2007). The integuments have the same thickness in number of cell layers, or the outer, and more rarely the inner, is thicker than the other. Pachychalazal ovules occur in both families (this study; Wiger, 1935; Robbertse *et al.*, 1986). Perichalazal ovules have been reported only in Anacardiaceae, in *Solenocarpus* (this study) and *Sclerocarya* (Spondiadoideae) (Robbertse *et al.*, 1986) and in *Semecarpus* (Anacardioideae) (this study).

The direction of ovule curvature has an impact on the distance of the micropyle from the placenta and the differentation of the micropylar region. In syntropous ovules the micropyle is close to the placenta. In antitropous ovules the micropyle is turned away from the placenta. Consequently, the distance has to be bridged either by an obturator, as in many Malpighiales (e.g. Merino Sutter, Forster & Endress, 2006), or by an extended micropyle. The second is found in Burseraceae. In the ovules of Burseraceae, the inner or single integument is conspicuously elongated and thickened above the nucellus and a long (S-shaped) endostomial micropyle is formed (this study; Wiger, 1935; Shukla, 1954; Narayana, 1959, 1960b). The tip of the (inner or single) integument extends into the base of the stylar canal. In contrast, in the syntropous ovules of Anacardiaceae the micropyle is initially closer to the placenta. However, the ovule is removed from the placenta by an unusually extensive growth of the funicle and the ovule is then only a small part in the resulting funicle–ovule complex (this study; Kelkar, 1958a, b; Grundwag, 1976; Robbertse *et al.*, 1986; von Teichman, 1988a, 1988b, 1991a, 1991b, 1992, 1993, 1994; von Teichman & van Wyk, 1996; von Teichman,1998; Carmello-Guerreiro & Sartori Paoli, 1999, 2005; Bachelier & Endress, 2007). The micropyle thus becomes distant from the placenta as in Burseraceae, but by a different mechanism. Anacardiaceae are characterized by a large and sometimes morphologically complicated funicle with various outgrowths. The funicle may be much larger than the ovule proper. However, in no representative in this study is the funicle larger than in *Amphipterygium* and *Pistacia* studied in Bachelier & Endress (2007), which further emphasises potential relationships between these two genera.

In Anacardiaceae, the funicle–ovule complex is conspicuously bent on the convex side of its curvature. In the region of the bend, the funicle–ovule complex is connected to the lower end of the PTTT at anthesis. Such a contact zone was termed a '*ponticulus*' (little bridge) by Joel & Eisenstein (1980) in *Mangifera*, because it may function as a shortcut in the pollen tube pathway between the style and ovule. At the site of the *ponticulus*, either the bend of the funicle–ovule complex directly projects into the base of the stylar canal or the base of the stylar canal bulges and is appressed to a saddle-shaped zone on the distal side of the bend of the funicle–ovule complex. A *ponticulus* is present in all species of Anacardiaceae studied here and thus appears as a prominent feature in the family (as also assumed by Robbertse *et al.*, 1986). Function of the *ponticulus* as a shortcut for the pollen tube pathway has been shown in some Anacardioideae (*Anacardium*, Copeland, 1961; *Mangifera*, Joel and Eisenstein, 1980; *Toxicodendron* Mill., Copeland & Doyel, 1940; *Pistacia*, Copeland, 1955; Grundwag & Fahn, 1969; Grundwag, 1976; Martínez-Pallé & Herrero, 1995; Shuraki & Sedgley, 1997). However, in *Pistacia* (Anacardioideae), although most pollen tubes grow toward the region of the *ponticulus*, a few may still follow the normal path via the placenta and penetrate the ovule via the strand of PTTT in the funicle (Shuraki & Sedgley, 1997). In Spondiadoideae, the *ponticulus* has never been shown to be a path for pollen tubes. They reach the funicle–ovule complex via the placenta in *Sclerocarya* and *Lannea*, despite the presence of a *ponticulus* (Robbertse *et al.*, 1986). At the site of the *ponticulus*, the funicle–ovule complex and the stylar canal are postgenitally connected at anthesis in *Anacardium* (this study) and *Mangifera* (Joel & Eisenstein, 1980), but seemingly only after anthesis in *Spondias dulcis* (this study).

This postgenital connection is achieved by meristematic activity at the base of the stylar canal (*Mangifera*, de Wet *et al.*, 1986) or at the contact site of the funicle–ovule complex (*Mangifera*, Joel & Eisenstein, 1980; *Pistacia*, Martínez-Pallé & Herrero, 1995) and may be triggered by pollination (Joel & Eisenstein, 1980) or not (Martínez-Pallé & Herrero, 1995). Chalazogamy has been reported in both subfamilies, such as in *Lannea* and S*clerocarya* of Spondiadoideae (Robbertse *et al.*, 1986) and *Anacardium* (Copeland, 1961), *Pistacia* (Copeland, 1955; Grundwag & Fahn, 1969; Grundwag, 1976; Martínez-Pallé & Herrero, 1995; Shuraki & Sedgley, 1997), *Rhus* (Grimm, 1912) and *Toxicodendron* (Copeland & Doyel, 1940) of Anacardioideae. Porogamy has only been reported in *Spondias* (Spondiadoideae) and *Semecarpus* (Anacardioideae) (Srinivasachar, 1940).

Because the *ponticulus* plays a role in pollen tube transmission, its protruding part (either the bend of the funicle–ovule complex or the end of the stylar canal) has been referred to as an obturator in *Anacardium* (Copeland, 1961) and *Mangifera* (Joel & Eisenstein, 1980). However, it does not exactly fit the original concept of an obturator (an outer part protruding into the micropyle, Baillon, 1858). But, sometimes, the base of the funicle close to the micropyle is so much expanded that it was interpreted as a ('funicular') obturator in *Amphipterygium* (Copeland & Doyel, 1940), *Pistacia* (Copeland, 1955; Grundwag & Fahn, 1969; Grundwag, 1976; Martínez-Pallé & Herrero, 1995) and *Lithraea* (Carmello-Guerreiro & Sartori Paoli, 2005). However, it has never been shown to be a path for the pollen tube in these genera and its main expansion is after anthesis in *Pistacia* (Grundwag, 1976; Bachelier & Endress, 2007). Anacardiaceae and Burseraceae are thus both lacking an obturator in the classical sense. In Anacardiaceae, another unusual development is the excessive enlargement of the integument(s) at the level above the nucellus, mainly by cell enlargement. These distal parts of the integument(s) attain the same foamy appearance as the bulk of the funicle–ovule complex. Only the nucellus and the part of the integument(s) immediately adjacent to the nucellus retain their 'normal' structure. In Anarcardiaceae, the single or outer integument then tends to form a loose hood and may have two large flaps, which are decurrent along the funicle and tend to envelop the inner part of the ovule and funicle base. In this case, the two (more or less symmetrical) margins of the flaps meet along the median symmetry plane of the ovule and appear in median longitudinal section as a single organ, probably corresponding to the large 'flap' described by Kelkar (1958a, b) (this study; Robbertse *et al.*, 1986). Such ovules with a long, bent funicle and a single or 'outer integument continuous with two labellate outgrowths of the massive funicle' were called 'raphe–chalazal ovules' by Robbertse *et al.* (1986), as an analogy to the perichalazal and pachychalazal seeds of Corner (1976).

Because of their different direction of curvature, the ovules of Burseraceae are more reminiscent of the structure of antitropous ovules of other groups (e.g. Kirkiaceae, Meliaceae, Simaroubaceae or Rutaceae) than of the syntropous ovules of Anacardiaceae. Two axile collateral placentae bearing two ovules as in Burseraceae are not so common in other Sapindales, whereas two axile placentae that are (almost) collateral with the two ovules becoming superposed, as in *Beiselia*, are known in Meliaceae (Wiger, 1935), Sapindaceae (Weckerle & Rutishauser, 2003) and Kirkiaceae (Bachelier & Endress, 2008). Bitegmic, antitropous and slightly campylotropous ovules with a longer and (sometimes) thicker inner integument and (long) S-shaped or zig-zag micropyle as in Burseraceae are also found in Kirkiaceae (Bachelier & Endress, 2008), Meliaceae, Simaroubaceae and Rutaceae (Wiger, 1935; Narayana, 1957, 1958; Narayana, 1960b; Nair & Sukumaran, 1960; Prakash, Lim & Manurung, 1977). In contrast, syntropous (campylotropous) ovules occur elsewhere in Sapindales only in Sapindaceae, in which the ovules have an obturator formed on the micropylar side of the funicle (Weckerle & Rutishauser, 2003, 2005). However, the fact that the inner integument is thicker than the outer one in some representatives of both families further supports this tendency in malvids (Endress & Matthews, 2006b).

In *Beiselia* and *Protium* (Burseraceae) occasionally only one ovule develops in the locule and is then in median position (this study). A single ovule per locule has also been reported in *Boswellia* (Sunnichan *et al.*, 2005) and in *Bursera* (Srivastava & Srinath, 1965). In contrast, in *Dracontomelon* (Anacardiaceae) a second, smaller ovule may develop at about the same level as the fertile ovule (this study); this second ovule is antitropous in contrast to the fertile syntropous ovule (this study). A second smaller and antitropous ovule in the inner angle of the locules was also found in *Spondias* (Baillon, 1874a). In *Dictamnus* L. (Rutaceae), there are two axile collateral and antitropous ovules, which develop above a single axile, median and syntropous ovule (Jadin, 1894). Furthermore, in earliest stages of development, the two collateral ovules in core Burseraceae appear to be syntropous as seen in tranverse sections of the gynoecium (J. B. Bachelier, pers. observ.). A similar observation of an early syntropy (directed downwards) was also made in *Protium serratum* (Colebr.) Engl. (Burseraceae) (Wiger, 1935: 114). Thus, it appears that in Burseraceae the ovules also tend to have an initial syntropous curvature, but soon become antitropous.

Fruit and seed

The structure of the pericarp has proved to be a good character for distinguishing Anacardioideae from Spondiadoideae (Wannan & Quinn, 1990; Wannan, 2006). In the *Spondias* type (Spondiadoideae), the endocarp consists of two cell layers. It is strongly lignified and its cells irregularly oriented (Wannan & Quinn, 1990). The *Spondias* type is functionally linked with the development of opercula and is also found in *Canarium* (core Burseraceae) (Wannan & Quinn, 1990; Martínez-Habibe, 2005). In the *Anacardium* type (Anacardioideae), the endocarp comprises four cell layers but is thinner than in the *Spondias* type and more discretely layered. In addition, it is not associated with opercula in fruit (Wannan & Quinn, 1990).

The differentiation of opercula in syncarpous fruits has been reported in many Spondiadoideae and in some Burseraceae (Martínez-Habibe, 2005; Wannan, 2006). Also common in the development of the fruit is the tendency to form a single seed. Reduced locules without a seed are sometimes still visible in the fruit. A completely different phenomenon is the development of secondary cavities by tissue degeneration in some Anacardiaceae. They may form large spaces in the pericarp, which have sometimes been mistaken for remains of reduced locules (Baillon, 1874b; Wannan & Quinn, 1990, 1991). However, their development in the pericarp can appear either irregular (*Harpephyllum*), more or less regular (*Schinus*) or regular (*Anacardium*, *Campnosperma*, *Choerospondias* B. L. Burtt. & A. W. Hill), sometimes alternating with the locules [*Allospondias* (Pierre) Stapf].

In Burseraceae, the calyx tends to persist during fruit development (Baillon, 1874a). In Anacardiaceae, in contrast, the persistent floral parts are diverse and are often involved in the dispersal of the diaspore. In addition, there is one clade in Anacardioideae in which fruits are primarily wind-dispersed (Pell, 2004; Pell & Mitchell, 2007). The free parts of the calyx may expand into wings similar to those of Dipterocarpaceae, although smaller, in *Astronium* Jacqu., *Loxostylis* A. Spreng. ex Rchb. and *Parishia* Hook. f. (Marchand, 1868; Ding Hou, 1978; Mitchell, 1995, 1997; Ashton, Kamariah & Said, 2003). Such wings or other devices for wind dispersal can also be formed by the expansion of the flower subtending bract in *Dobinea* Buch.-Ham. ex D. Don and *Campylopetalum* (Dobineeae, Forman, 1954), the free corolla parts in *Gluta* spp. and *Swintonia* Griff. (Marchand, 1868; Ding Hou, 1978; Ashton *et al.*, 2003) or the edges of carpels in *Dobinea* (Forman, 1954), *Blepharocarya* (Wannan *et al.*, 1987) and *Loxopterygium* and *Schinopsis* Engl. (Mitchell, 1995, 1997), the flattened peduncle of the infloresences as in *Amphipterygium* and *Orthopterygium* Hemsl. (Bachelier & Endress, 2007) or the elongated and hairy infructescence axes, including pedicels, of aborted flowers, as in *Cotinus* (Engler, 1892). In *Amphipterygium* and *Blepharocarya*, a cupule is formed by expansion and fusion of bracts and pedicels, but the dispersal units are different: fruit in *Blepharocarya* and infructescences in *Amphipterygium*, both adapted to wind dispersal (Airy Shaw, 1965; Bachelier & Endress, 2007). In *Anacardium* and *Semecarpus* the fruit stalk also expands after anthesis into a fleshy structure, but it is an adaptation for bat dispersal (Ding Hou, 1978; Mitchell & Mori, 1987). In Burseraceae (Protieae and Burserinae), a pseudoaril is formed by the mesocarp (Engler, 1896; Martínez-Habibe, 2005) and is an adaptation for bird dispersal (Janson, 1983); the largest diaspores may also be dispersed by primates (Stevenson, Link & Ramírez, 2005). In Burseraceae, the stigmatic head also tends to be persistent and remain united, although sometimes off-centred by unequal development of the locules as in *Santiria* (Ashton *et al.*, 2003). In Anacardiaceae, styles and stigmas are more or less persistent. In Spondiadoideae, the (contiguous) styles and stigmas are shifted toward the periphery of the fruit by the development of the central region of the ovary (Mitchell & Daly, 1991; Wannan & Quinn, 1991; Mitchell *et al.*, 2006). The former centre of the floral apex exposed at anthesis remains conspicuous in fruit (e.g. *Spondias purpurea* and *Pleiogynium*) or becomes exposed in fruit if the styles and stigmas were contiguous at anthesis (e.g. *Spondias dulcis* and *Dracontomelon*) (this study; J. B. Bachelier, pers. observ.). In contrast, in Anacardioideae, the united bases of the styles tend to persist on top of the fruit (J. B. Bachelier, pers. obervs.). Abscission of stigmatic branches and a differentiated abscission zone are not often reported, but may occur in both subfamilies, in Spondiadoideae, for example, in *Sclerocarya* (illustrations in von Teichman & Robbertse, 1986) and in Anacardioideae, in *Anacardium* (Wunnachit *et al.*, 1992), *Mangifera* (von Teichman, Robbertse & Schoonraad, 1988), *Pistacia* and *Amphipterygium* (Bachelier & Endress, 2007).

Parthenocarpic fruit development is another trend present in both families (Copeland & Doyel, 1940; Copeland, 1955; Kelkar, 1958a; Copeland, 1959, 1961; Srivastava, 1968; Grundwag, 1976; von Teichman & Robbertse, 1986; Bachelier & Endress, 2007; J. Bachelier, pers. observ.). It has been shown in both *Bursera* and *Pistacia* that the development of sterile fruits is a strategy that reduces seed predation before dispersal (Verdú & García-Fayos, 2000; Ramos-Ordoñez, Márquez-Guzmán & Del Coro Arizmendi, 2008).

Histology

Unicellular and lignified hairs and glandular hairs with uniseriate stalks and multicellular heads (also

referred to as club-shaped hairs or snail hairs) are frequent in both families. These observations are supported and well illustrated by previous works (Fritsch, 1908; Metcalfe & Chalk, 1950; von Teichman & Hardy, 1992). Less frequently found are hairs with two branches as in the T-shaped hairs in *Protium* (Burseraceae), more branches as in *Santiria* or stellate hairs in *Campnosperma* and *Lannea*. Peltate hairs (scales) have only been observed in *Campnosperma* (this study; Metcalfe & Chalk, 1950). Unicellular hairs on stamens are not frequent but are present in both families, on filaments (*Anacardium*, *Beiselia*) and anthers (*Amphipterygium*, *Canarium*, *Santiria*), as also shown for other Sapindales (Endress & Stumpf, 1991).

In both families, vasculature tends to be poorly differentiated at anthesis, especially on the dorsal side of the carpels. Resin canals are also present in flowers of both families. They regularly develop in the phloem of the vascular bundles and thus appear to be dorsal with regard to the xylem (this study; Venning, 1948; Wannan & Quinn, 1991). In most of the species studied, such resin (secretory) canals are present in the perianth organs. In the androecium, they are consistently present in Burseraceae, either in the filament, the anther or both, but lacking in Anacardiaceae, except for the anthers of a few Spondiadoideae (*Pleiogynium* and *Tapirira*) (see Androecium). In both families, the resin canals are sometimes less developed in the anthetic gynoecium than in the fruit (Venning, 1948; J. B. Bachelier, pers. observ.). They are lacking in the ovule bundle and sometimes in the small bundles. More rarely, they are well developed but do not appear to be associated with the vasculature (this study; Venning, 1948; Wannan & Quinn, 1991).

Special mucilage cells with a conspicuous swollen and layered inner tangential wall (for term, see Matthews & Endress, 2006) are present only in the epidermis and subepidermis of the sepals and floral base of some core Burseraceae and, more rarely, also in the parenchyma of the floral base as in *Commiphora* or in petals as in *Canarium*. However, such cells are also found in the leaves of both families (Metcalfe & Chalk, 1950; Matthews & Endress, 2006).

Hairs in other Sapindales are common, especially glandular hairs with uniseriate multicellular stalks and uni- or multiseriate multicellular heads (Metcalfe & Chalk, 1950; Ronse de Craene & Haston, 2006). The glandular hairs can be more or less developed and conspicuous, depending on the size of their heads and density. Such hairs are found, for instance, on the sepals and bracts of *Peganum* L. (Nitrariaceae; Ronse de Craene, De Laet & Smets, 1996) and are similar to those found on *Beiselia* petal tips. A carpet of glandular hairs is also found at the base of the petals in *Kirkia* (Kirkiaceae) but they appear to have a multiseriate multicellular stalk (Bachelier & Endress, 2008). In Malvaceae, similar dense carpets of hairs are found at the base of petals and are nectariferous (Vogel, 2000).

Poorly differentiated vasculature in the dorsal region of the carpels has often been noted in other Sapindales (Ronse de Craene & Haston, 2006). Secretory glands or ducts are common in Sapindales (Wiger, 1935). They have been given a strong systematic value, depending on their development (Engler, 1931d). Resin canals as in flowers of Anacardiaceae and Burseraceae are present elsewhere in Sapindales only in Simaroubaceae (J. B. Bachelier, pers. observ.) and in some Sapindaceae (J. B. Bachelier, pers. observ.). Sometimes they are referred to as 'laticiferous' canals in Sapindaceae (see illustrations in Weckerle & Rutishauser, 2005). Large secretory structures are also present in the flowers of Rutaceae and Meliaceae but, there, they never develop canals. They remain spherical and are often referred to as 'oil glands' (Engler, 1931d).

Special mucilage cells as found in Burseraceae are present in half of the families of the order, but are not necessarily frequent in any family. They occur elsewhere in Sapindales in flowers of Kirkiaceae (Bachelier & Endress, 2008), Simaroubaceae (*Soulamea* Lam., J. B. Bachelier, pers. observ.), Nitrariaceae (*Nitraria* L., J. B. Bachelier, pers. observ.) and Sapindaceae (Matthews & Endress, 2006). Such cells are more commonly observed in the leaves of most sapindalean families (Metcalfe & Chalk, 1950; Matthews & Endress, 2006).

Floral structure and systematics

Which floral structural features characterize the clades and subclades of the study group that have been retrieved in molecular studies (Fig. 1; Terrazas, 1994; Clarkson *et al.*, 2002; Aguilar-Ortigoza & Sosa, 2004; Pell, 2004; Weeks *et al.*, 2005; Wannan, 2006; Muellner *et al.*, 2007)?

Burseraceae

Burseraceae are distinct from Anacardiaceae in the following features:

1. Gynoecium never pseudomonomerous or monomerous (never monosymmetric).
2. Carpel tips free but forming a stigmatic head by postgenital fusion (only contiguity, without fusion, in *Canarium* of this study).
3. Stigmatic head forming an external compitum (with abundant secretion at anthesis).
4. Symplicate zone not clearly forming a compitum.
5. Ovules two, antitropous, (mostly) campylotropous.

6. Vasculature in the gynoecium with inverse synlateral bundles in the ovary septa with dorsal xylem and a ventral resin canal in the phloem (this study; Stevens, 2001 onwards).

Core Burseraceae

Core Burseraceae are distinct from *Beiselia* in the following features.

1. Special mucilage cells (in epidermis and hypodermis) present in sepals and floral base (vs. mucilage cells lacking in flowers).
2. Symplicate zone extensive, encompassing part of the ovary and style (former centre of floral apex enclosed in the ovary) (vs. symplicate zone only above the ovary, former centre floral apex in the style).
3. Synascidiate zone extending up to about the midpoint of the locules (vs. synascidiate zone extending beyond the ovary).
4. Ovules two, exactly collateral, with micropyles contiguous (vs. the two ovules not collateral but superposed).
5. Ovule vascular bundle extending into the single outer integument(s) [vs. ending below integument(s)].

Among the subclades of core Burseraceae, the monophyletic Canarieae are distinct from the monophyletic Protieae in having trimerous flowers (vs. pentamerous) (Lam, 1932a, b), with a thick cup, stiff petals and stamens of type 2 (vs. type 1) (see Discussion on androecium), hairs on the anthers and a globose ovary (this study). In Protieae and Canarieae, only single genera or single tribes were studied (Protieae; Daly, 1992, 2007; Canarieae; Lam, 1932a, b; Martínez-Habibe, 2005, on fruits). From our study, Canarieae seem to have more autapomorphies than Protieae.

Anacardiaceae

Anacardiaceae are distinct from Burseraceae in the following features.

1. Petals with ventral longitudinal ridges (*Anacardium, Mangifera, Semecarpus* and *Pleiogynium*).
2. Androecium monosymmetric (some Anacardioideae).
3. Gynoecium commonly pseudomonomerous or monomerous, thus gynoecium monosymmetric.
4. Stigmatic head absent (except for *Dracontomelon*) (this study).
5. External compitum formed by contiguity (not fusion) of the free carpel tips (*Pleiogynium, Spondias* and *Buchanania*) (this study).
6. Ovules syntropous, anatropous at anthesis (rarely campylotropous, *Semecarpus*).
7. Funicle bent, long, ovule being part of a funicle–ovule complex ('raphe–chalazal ovule' of Robbertse *et al.*, 1986).
8. Ovules perichalazal (*Solenocarpus* and *Semecarpus*) (this study).
9. Outer or single integument hood-shaped, forming loose, large flaps, which are decurrent along the funicle (this study).
10. Micropyle not closed at anthesis in some taxa (*Pistacia, Dracontomelon* and *Spondias dulcis)* (this study).
11. Pollen tube growing through chalaza (chalazogamy) (Grimm, 1912; Copeland & Doyel, 1940; Copeland, 1955, 1961; Grundwag, 1976; Robbertse *et al.*, 1986; Martínez-Pallé & Herrero, 1995; Shuraki & Sedgley, 1997).
12. Sepal lateral vascular bundles tending not to form separate (not synlateral) traces in the floral base (*Dracontomelon, Spondias, Pleiogynium, Anacardium*, but also *Bursera*) (this study).
13. Special mucilage cells lacking in the flowers (this study).

Among the subgroups of Anacardiaceae, Anacardioideae form a well-supported clade (Terrazas, 1994; Aguilar-Ortigoza & Sosa, 2004; Pell, 2004; Pell & Mitchell, 2007). Spondiadoideae are either a clade (Pell, 2004; Wannan, 2006; Pell & Mitchell, 2007) or a grade (Aguilar-Ortigoza & Sosa, 2004; Wannan, 2006). Anacardioideae are distinguished from Spondiadoideae by a pseudomonomerous (or monomerous) gynoecium, thus gynoecial monosymmetry (vs. pluricarpellate, thus polysymmetric), not clearly synascidiate ovary (vs. strongly synascidiate) (see Discussion on gynoecium). *Buchanania* is unplaced. It is either in Spondiadoideae (Pell & Mitchell, 2007) or, if Spondiadoideae are a grade, *Buchanania* appears as sister to Anacardioideae (Aguilar-Ortigoza & Sosa, 2004; Wannan, 2006). In its floral structure, *Buchanania* shares with Spondiadoideae isomerous, obdiplostemonous flowers and, with Anacardioideae, a basal ovule insertion.

Clade of Burseraceae plus Anacardiaceae

Burseraceae and Anacardiaceae share the following features:

1. Flowers isomerous, obdiplostemonous.
2. Sepals with three vascular traces.
3. Petals becoming longer than sepals in bud and protecting the other floral organs up to anthesis.
4. Petals with acute tips bent inwards, with valvate aestivation in bud (Burseraceae, some Spondiadoideae, some Anacardioideae).
5. Petal margins in bud with postgenital coherence, formed by interdentation of papillate epidermis and cuticular ornamentation.

6. Petals with a single vascular trace.
7. Similar variation in number of stamens (decrease to one and increase to three whorls).
8. Similar variation in number of carpels (increase and probably decrease from five, up to double number (*Beiselia*, Burseraceae and *Pleiogynium*, Anacardiaceae) and down to two (*Bursera, Commiphora*, Burseraceae) or one (Anacardiaceae).
9. Gynoecium syncarpous (never apocarpous).
10. Carpel distal parts always free but often contiguous (most Spondiadoideae, and *Canarium*, Burseraceae) or postgenitally united (most Burseraceae; *Dracontomelon*, Anacardiaceae).
11. Synascidiate zone extending beyond the locules (*Beiselia*, Burseraceae; Spondiadoideae).
12. Ovules never more than one or two per locule.
13. Ovules campylotropous at anthesis (most Burseraceae; *Semecarpus*, Anacardioideae).
14. Ovules pachychalazal after anthesis, in some cases already at anthesis (this study; Corner, 1976; Robbertse *et al.*, 1986; von Teichman & van Wyk, 1991; von Teichman, 1998).
15. Ovules sometimes unitegmic.
16. Integument(s) strongly and irregularly lobed and forming an irregular, slit-shaped micropyle.
17. Ovary with dorsal vascular bundle poorly differentiated.
18. Styles and stigmas persistent during fruit development.
19. Seed only one per locule (two only in *Pseudodacryodes* R. Pierlot, Burseraceae, Martínez-Habibe, 2005).
20. Endocarp with two sclerified cell layers (plus two additional ones only around the fertile locule, Wannan & Quinn, 1991).
21. Floral vascular bundles associated with resin canals, except for the ovule bundle.

Within the clade of Anacardiaceae plus Burseraceae, most features shared by Burseraceace and Anacardiaceae are shared by Spondiadoideae of Anacardiaceae and Burseraceae (e.g. isomerous flowers and obdiplostemony) and could be seen as plesiomorphies (or synapomorphies) (see below, clade of Anacardiaceae plus Burseraceae and Kirkiaceae). In addition, *Beiselia*, sister to core Burseraceae, shares with *Dracontomelon* and some other Spondiadoideae (Anacardiaceae) features that could be seen as plesiomorphies (or synapomorphies) of the clade of Burseraceae plus Anacardiaceae, such as the synascidiate zone extending beyond the ovary and the free stigmas and styles being postgenitally united (see below, clade of Burseraceae plus Anacardiaceae, plus Kirkiaceae). In contrast, most of the rare similarities shared by Burseraceae and Anacardiaceae occur in core Burseracae and Anacardioideae and may be seen as convergent autapomorphies (e.g. haplostemony and unitegmy).

In sum, Burseraceae and Anacardiaceae, long placed in different orders (Engler, 1892, 1896, 1931d), have been shown to form a clade by molecular studies (Terrazas, 1994; Gadek *et al.*, 1996; Pell, 2004; Pell & Mitchell, 2007) and this close relationship is also suggested by floral structural features. This is not only emphasized by the general floral structure of the two families but also by the existence of the genus *Beiselia* (Burseraceae).

Clade of Burseraceae plus Anacardiaceae plus Kirkiaceae

Kirkiaceae appear to be sister to Anacardiaceae plus Burseraceae (Muellner *et al.*, 2007). As the topology of other families of Sapindales is not well resolved (Gadek *et al.*, 1996; Bakker *et al.*, 1998; Pell, 2004; Muellner *et al.*, 2007), a tentative evaluation of character evolution in the Anacardiaceae–Burseraceae clade can only be carried out by comparing it with Kirkiaceae. Floral structure in Kirkiaceae was studied by Bachelier & Endress (2008) in view of a comparison with Anacardiaceae and Burseraceae. In general, Kirkiaceae exhibit more similarities with Burseraceae than with Anacardiaceae, which suggests that Burseraceae are more conservative and have kept more plesiomorphies, whereas Anacardiaceae have more autapomorphies, especially in the gynoecium. This is also suggested when compared with the other families of Sapindales, in which such putative plesiomorphies as in Burseraceae are also present.

The following features are potential autapomorphies for Anacardiaceae (not present in Burseraceae and Kirkiaceae):

1. Monosymmetric androecium (former Anacardieae).
2. Pseudomonomerous or monomerous (monosymmetric) gynoecia.
3. One ovule per carpel, with median placenta.
4. Placenta basal (e.g. *Buchanania*, *Anacardium*, *Mangifera*, *Pistacia, Lithraea* and *Amphipterygium*).
5. Ovule much smaller than locule at anthesis.
6. Ovule syntropous.
7. Ovule anatropous (not campylotropous) at anthesis.
8. Outer or only integument enlarged and extremely large-celled (hypertrophied) beyond the nucellus.
9. Funicle long and forming with the ovule a funicle–ovule complex.
10. Presence of a *ponticulus*.
11. Presence of chalazogamy.

12. Micropyle often not tightly closed.
13. Special mucilage cells in floral organs absent.

One of the most unusual characters that is shared by Kirkiaceae, *Beiselia* (sister to core Burseraceae) and Spondiadoideae (Anacardiaceae) is the presence of an extensive synascidiate region, which extends far beyond the ovary and the formation of a conspicuous more or less convex plate between the carpels above the ovary. It is not known from any other Sapindales and may be a synapomorphy for the three families (see also Bachelier & Endress, 2008). In addition, in some Kirkiaceae, *Beiselia* and *Pleiogynium* (Spondiadoideae), taxa with an increased number (8–13) of carpels occur. This is less consistent than the first feature (present only in a smaller part of Kirkiaceae and Spondiadoideae) and thus may be viewed just as an apomorphic tendency.

CONCLUSIONS

The present comparative study of floral structures is the first in the clade of Anacardiaceae plus Burseraceae. Both the sister relationship of Anacardiaceae and Burseraceae and the monophyly of each family, as found in molecular phylogenetic studies, are supported by floral structural features. In Anacardiaceae, Anacardioideae are more uniform than Spondiadoideae. The position of *Buchanania*, either as sister to Anacardioideae or nested in Spondiadoideae, as indicated by molecular phylogenetic studies, are both supported by floral structures. In Burseraceae, the position of *Beiselia* as sister to the remainder of Burseraceae and the monophyly of core Burseraceae are strongly supported. A consistent feature of Anacardiaceae is the presence of a *ponticulus* on the dorsal side of the funicle–ovule complex. A consistent feature of Burseraceae is the presence of a stigmatic head formed by postgenital union of the free carpel tips.

Our results are a further step to a better understanding of the floral evolution in Sapindales. The strong similarities of the gynoecium structure between some Spondiadoideae (Anacardiaceae) and *Beiselia*, sister to the remainder of Burseraceae, show that molecular phylogenetic studies including unstudied early branching representatives of each family are needed. This should help to resolve better the relationships between and within the two families and allow reconstruction of floral character evolution in the clade of Anacardiaceae and Burseraceae within Sapindales.

ACKNOWLEDGEMENTS

The Forestry Department of Brunei Darussalam is thanked for assistance during a field-trip collection, and Joffre Haji Ali Ahmad for organizing and supervising the collection trips, Jangarun Eri for expertise in the field and Ariffin for help in plant identifications at BRUN. The Georges-und-Claraz-Schenkung is thanked for financial support of the field trip. We acknowledge Marie-Françoise Prévost (French Guyana), Jérôme Munzinger (New Caledonia) and Ursula Hofmann (University of Göttingen) for collecting material and Paul A. Cox, Tropical Botanical Garden of the United States Hawaii, for hosting the second author. Sir Peter Crane, Royal Botanic Gardens, Kew, is thanked for flowering material. Eduard Ramp and Caroline Weckerle are gratefully acknowledged for allowing the authors to study some of their microtome sections of Rutaceae and Simaroubaceae and of Sapindaceae, respectively. We also thank Rosemarie Siegrist, Patrick Wallin and Kim Phillips for support with microtome sectioning, Urs Jauch for support with the SEM, and Mary Endress for reading the manuscript. Gerhard Prenner and Anton Weber are thanked for reviewing the manuscript.

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